

Possibilities for producing compact floricultural crops

Susana M.P. Carvalho, Filip van Noort, Romke Postma & Ep Heuvelink





Possibilities for producing compact floricultural crops

Susana M.P. Carvalho¹, Filip van Noort², Romke Postma³ & Ep Heuvelink¹

¹ Wageningen University, Isg. Tuinbouwketens

² Wageningen UR Greenhouse Horticulture

³ Nutrient Management Instituut

© 2008 Wageningen, Wageningen UR Greenhouse Horticulture

All rights reserved. No part of this publication may be reproduced, stored in a retrieval system or transmitted, in any form or by any means, electronic, mechanical, photocopying, recording or otherwise, without the prior written permission of Wageningen UR Greenhouse Horticulture



Wageningen UR Greenhouse Horticulture

Adres : Bornsesteeg 65, 6708 PD Wageningen, The Netherlands
: P.O. Box 16, 6700 AA Wageningen, The Netherlands
Tel. : +31 317 - 47 70 01
Fax : +31 317 - 41 80 94
E-mail : greenhousehorticulture@wur.nl
Internet : www.greenhousehorticulture.wur.nl

Table of contents

	page
List of abbreviations	1
Summary	3
Samenvatting	5
1 Aim and outline of the report	7
2 Factors affecting stem elongation in floricultural crops	9
2.1 Aboveground growth conditions	9
2.1.1 Temperature (average, DIF, DROP)	9
2.1.2 Light intensity	11
2.1.3 Light quality (Red/Far-red ratio; Blue light)	12
2.1.4 Photoperiod	13
2.1.5 Relative humidity	14
2.1.6 CO ₂ concentration	14
2.1.7 Plant density and pot size	14
2.1.8 Relevant interactions between climate conditions	14
2.2 Growth conditions in the root environment	15
2.2.1 Nutrients (N, P, Ca)	15
2.2.2 Compalox	19
2.2.3 EC and water availability	20
2.2.4 Substrate (use of clay)	20
2.3 Stress factors (mechanical stress, cold water application)	21
2.4 Plant growth regulators	22
2.4.1 Plant hormones	22
2.4.2 Chemical growth retardants	23
3 Underlying mechanisms behind internode elongation	27
3.1 Control of cell growth	27
3.2 GA-metabolism	27
3.3 Photoassimilates	28
3.4 Water availability	28
3.5 General hypothesis for stem elongation process	29
4 Practical applications (alternatives to chemical growth retardants)	31
4.1 DIF and DROP treatments	31
4.2 Manipulation of light quality	32
4.3 Nutrients and water management	33
4.4 Plant breeding	33
4.5 Conclusions	34
5 Knowledge gaps and future research	37
Literature	39

Appendix I.	1 p.
Appendix II.	1 p.
Appendix III.	1 p.
Appendix IV.	1 p.
Appendix V.	1 p.
Appendix VI.	1 p.
Appendix VII.	1 p.

List of abbreviations

ADT	=	Average day temperature
CCC	=	Chlormequat
DIF	=	DIFference between day temperature and night temperature
DROP	=	Short-term temperature reduction
DT	=	Day temperature
EC	=	Electrical conductivity
ER	=	Elongation requirements
EOD	=	End-of-day
ESD	=	Extreme short-days
FR	=	Far-red light
GA	=	Gibberellins
HPS	=	High pressure sodium lamps
IAR	=	Internode appearance rate
LED	=	Light-emitting diodes
NT	=	Night temperature
PGR	=	Plant-growth retarding chemicals
PPFD	=	Photosynthetic photon flux density
RH	=	Relative humidity
SER	=	Stem elongation rate
TDM	=	Total plant dry mass

Summary

The control of stem length is particularly important in the production of ornamental plants since there are strict quality specifications for height. To achieve more compact and better-shaped plants chemical growth retardants are commonly used. However, their application is costly and environment- unfriendly. The need to find effective environment-friendly strategies for regulating plant height is one of the goals in future production of floricultural crops. This study aimed at gathering and analysing the most relevant information available in literature concerning the factors affecting stem length and understanding the underlying mechanisms behind stem elongation. That knowledge was further integrated to define guidelines for producing compact plants with a minimum input of chemical growth retardants.

The factors involved in stem elongation were divided in: aboveground growth conditions (i.e. climate conditions, plant density and pot size), conditions in the root environment (nutrients and water availability, EC and substrate), stress factors (mechanical conditioning and cold water stress) and plant growth regulators (plant hormones and chemical growth retardants). Several of these factors have a significant effect on internode elongation. However, in most cases it will not be one single measure that will result in a compact plant. This study provides several possibilities that, in combination, can provide the desired height control. Part of these measures is fairly easy to apply and require little or no investment and relatively small interventions in the cropping systems. Growing plants at a negative DIF (i.e. higher night than day temperature) or at a high R/FR ratio (continuously or only at the end of the light period) are promising nonchemical strategies for reducing stem elongation of many ornamental plants. Nevertheless, so far only the temperature manipulation has been widely implemented in commercial production. The reasons why photosensitive films (filtering far-red light) are not commercially used are mainly due to their negative effect on plant growth (biomass increase) and quality (as a result of a lower light intensity) and a delay in time to flowering. The use of a negative DIF provides effective growth control in periods of lower temperatures and low light conditions. On the other hand, spectral filters are most feasible during high light summer situations, as in those situations the lower light intensity that reaches the crop canopy, is of less importance for plant growth and quality. To achieve more effective results, these measures can be combined with low nutrient availability, reduced water availability, mechanical stress and/or daylength control. Plant breeding might also offer good possibilities for developing dwarf cultivars.

Although many studies have been conducted on this topic only few have focused on understanding the physiological basis of stem elongation. In the current report we hypothesize that 'elongation requirements' (ER) are needed for the internode elongation process. Their exact nature is not known but they are most likely both photoassimilates and inactive forms of gibberellins (GA). These ER are accumulated during the day and this process is governed by day temperature, whereas night temperature governs their conversion into elongation. Water availability is required for the elongation process, which becomes limited by the cell wall elasticity, governed both by day and night temperature. This report ends with the identification of several knowledge gaps and the presentation of guidelines for future research.

Samenvatting

Het beheersen van de lengtegroei van een plant is een belangrijk aandachtspunt in de sierteelt omdat er strenge kwaliteitsspecificaties bestaan voor de lengte van siergewassen. Chemische remmiddelen worden vaak gebruikt om een meer compact en beter gevormde plant te telen maar dit gebruik is duur en belast het milieu. Het vinden van effectieve en milieuvriendelijke strategieën voor het beheersen van de plantlengte is een aandachtspunt voor toekomstige productiemethodes in de sierteelt. In dit literatuuronderzoek is de meest relevante beschikbare informatie over de factoren die de lengtegroei van planten beïnvloeden samengebracht en geanalyseerd. Daarbij wordt nadrukkelijk ook aan de onderliggende processen met betrekking tot lengtegroei aandacht gegeven. Deze kennis wordt vervolgens geïntegreerd zodat richtlijnen voor het produceren van compacte planten met een zo gering mogelijk gebruik aan groeiregulatoren opgesteld konden worden.

De factoren die van belang zijn voor stengelstrekking zijn opgedeeld in: bovengrondse groeiomstandigheden (klimaatomstandigheden, plantafstand en potmaat), omstandigheden in het wortelmilieu (nutriënten, waterbeschikbaarheid, EC en substraat), stress factoren (mechanische stress en koud water stress), en plantengroeiregulatoren (plantenhormonen en chemische remmiddelen). Een aantal van deze factoren heeft een significant effect op de strekking van internodia, maar meestal is het niet slechts één factor die een fraaie, compacte plant zal geven. Dit rapport geeft een aantal voorbeelden van factoren, die in combinatie met elkaar, de gewenste controle over de lengtegroei kunnen geven.

Sommige maatregelen genoemd in deze studie zijn vrij eenvoudig toe te passen: ze vragen geen of slechts een kleine investering en betreffen betrekkelijk kleine ingrepen in het teeltsysteem. Het telen van planten bij een negatieve DIF (een hogere nacht- dan dag temperatuur) of onder een hoge R/FR (rood/verrood) verhouding (voortdurend of alleen aan het eind van de lichtperiode) zijn veelbelovende maatregelen om de lengtetoeename van veel sierplanten te verminderen zonder chemisch in te grijpen. In de praktijk zijn alleen de temperatuuraanpassingen al veelvuldig toegepast. Dat fotoselectieve folies (wegfilteren van verrood licht) niet commercieel in gebruik zijn, is voornamelijk te wijten aan de negatieve effecten van deze folies op plantengroei en -kwaliteit (lagere lichtintensiteit) en de vertraging in bloei die ze kunnen geven. Gebruik van negatieve DIF is alleen mogelijk gedurende periodes van lagere temperatuur en licht. Daarentegen zijn fotoselectieve folies meer van toepassing tijdens zomeromstandigheden met hoge lichtniveaus, omdat dan de lagere lichtintensiteit die het gewas bereikt, van minder belang is voor groei en kwaliteit (er is al genoeg licht). Voor een meer effectieve beheersing van de strekkingsgroei kunnen deze maatregelen ook gecombineerd worden met een lager nutriënteniveau, een verminderde beschikbaarheid van water, mechanische stress en/of het aanpassen van de daglengte. Genetica en veredeling kunnen ook goede mogelijkheden bieden om dwergvariëteiten te ontwikkelen.

Hoewel er op dit gebied veel onderzoek verricht is, wordt er zelden gericht verdieping gezocht, richting het begrijpen van de fysiologische principes die achter stengellengte-toename schuilgaan. In deze rapportage wordt als hypothese naar voren gebracht dat 'strekkingseisen' (elongation requirements; ER) aanwezig moeten zijn om internodiumstrekking mogelijk te maken. Wat deze ER precies zijn is niet bekend maar zowel foto-assimilaten als inactieve vormen van gibberellinen (GA) zijn mogelijke voorbeelden hiervan. Deze ER worden aangemaakt gedurende de dag onder invloed van de dagtemperatuur, terwijl de nachttemperatuur hun conversie naar daadwerkelijke strekking beheerst. Waterbeschikbaarheid is noodzakelijk voor het strekkingsproces, dat gelimiteerd wordt door de celwandelasticiteit; deze laatste wordt beïnvloed door zowel de dag- als de nachttemperatuur. Dit rapport eindigt met het vaststellen van deelgebieden waarop kennis ontbreekt en stelt richtlijnen op voor toekomstig onderzoek.

1 **Aim and outline of the report**

This literature study aims at giving an overview of the factors involved in stem elongation and the underlying physiological mechanisms behind this process. It is also our aim to identify the gaps in literature and use this integrated knowledge as a first step towards sustainable production of compact ornamental plants and cut flowers.

This report is divided in four chapters. In **Chapter 2** we describe in depth all the factors that have been identified in literature as having an effect on stem elongation. These factors are divided into growth conditions (aboveground and in the root environment), stress factors (induced mechanically or with cold water) and plant growth regulators. In **Chapter 3** we focus on the understanding of the underlying physiological mechanisms behind the control of elongation growth and a general hypothesis for internode elongation is formulated. Based on the knowledge build up in the previous chapters, **Chapter 4** deals with summarizing and discussing the possible alternatives to chemical growth retardants for producing compact floricultural crops. Finally, in the last section (**Chapter 5**) the gaps in current knowledge and suggestions for future research are presented.

2 Factors affecting stem elongation in floricultural crops

Total stem length is the result of the number of internodes and the length of these internodes (Pearson *et al.*, 1995). Thus, the stem elongation process is strongly correlated with both internode appearance rate (IAR, equal to leaf unfolding rate) and internode elongation rate. IAR in most species is predominantly controlled by temperature, and to a much lesser extend (and in a limited number of species) by light intensity. In species with a determinate growth pattern new internodes (same as new leaves) stop to be formed when flowers are initiated (e.g. chrysanthemum, kalanchoe, liliun, poinsettia etc). Therefore, conditions that promote flowering (e.g. the most inductive photoperiods or optimum temperatures) will result in fewer internodes and consequently shorter plants. This is also the case when providing high light intensity in species with a facultative irradiance response (i.e. plants in which flower initiation is enhanced at higher daily light integral) or providing an 'optimal' cooling treatment to species with a facultative or obligate vernalization response. In both cases plants will initiate flowers at an earlier physiological stage, which leads to fewer internodes (E. Runkle; pers. comm.). After flower initiation has occurred in plants with a determinate growth pattern, the increase in stem length depends on internode elongation only. In this literature study we will focus on the factors that influence internode elongation as the mechanisms behind this process are more complex than the ones involved in the appearance of new internodes and, therefore, a more detailed analysis is needed.

2.1 Aboveground growth conditions

Interest in controlling plant height in greenhouse production of ornamental plants in an environmentally friendly way has initiated extensive research on how temperature (Bachman & McMahan, 2006; Stavang *et al.*, 2006) and light quality (Bachman & McMahan, 2006) can be used to control plant morphology. Efforts have been concentrated on these two climate conditions since they have demonstrated a strong influence on internode elongation. Most of the literature available on the control of stem elongation is, therefore, related to these two climate conditions. However, besides these two factors also light intensity, photoperiod, relative humidity and CO₂ concentration can play a role. Plant density and pot size are cultivation measures that can also influence internode elongation, as a result of their indirect effect on the microclimate within the crop,.

2.1.1 Temperature (average, DIF, DROP)

Temperature manipulation to regulate stem elongation is used in practice for a wide range of plant species. It is known that average daily temperature (ADT) influences the internode elongation in some ornamentals, such as *Impatiens hawkeri* Bull. (Erwin *et al.*, 1992a) and *Petunia x hybrida* Hort. Vilm. Andr. (Ludolph, 1992). In chrysanthemum, higher ADT increases stem elongation rate resulting in taller plants and this is due to both higher number of internodes and longer internodes (Langton & Cockshull, 1997b; Langton, 1998). Also in *Kalanchoe* it was found that plants grown under a constant temperature of 26°C were 60% taller than plants grown at constant 18°C (Carvalho *et al.*, 2006).

Since stem elongation rate is not constant during a day/night cycle, diurnal temperature alternations have been commonly used to control plant height based on the DIF concept: the difference between day (DT) and night (NT) temperature (Fig. 1; reviewed by Myster & Moe, 1995). In general, a warm night and a cold day results in short compact plants, while a warm day and a cold night increases stem elongation and thus gives taller plants. The observation that stem length shows a different response to temperature during the photoperiod compared with nyctoperiod was first investigated for tomato plants and termed 'thermoperiodicity' (Went, 1944). Since then, it has been reported for a wide range of plant species (e.g. Heuvelink, 1989; Erwin & Heins, 1995; Myster & Moe, 1995). Erwin *et al.* (1989) introduced the DIF concept when they found that plants of *Lilium longiflorum* Thunb. had the same final height when grown at the same DIF (using 25 combinations of DT and NT ranging from 14 to 30 °C), regardless

of the ADT. According to these authors, DT and NT influenced plant height in opposite ways. Increasing DT increased plant height, whereas increasing NT decreased plant height. Therefore, temperature combinations resulting in a negative DIF produced plants that were shorter than those grown under a positive DIF. Many subsequent studies have shown similar results, to those of Erwin *et al.* (1989), for many plant species (reviewed by Myster & Moe, 1995; Appendix 1) and a strong positive correlation between internode length and DIF has been observed (e.g. Heuvelink, 1989; Erwin & Heins, 1995; Myster & Moe, 1995). Thus, as later suggested the DIF effect on stem length was exclusively a result of its influence on internode elongation since terminal flowers had already been initiated and, therefore, the final number of internodes had been determined before the start of the treatment (Langton & Cockshull, 1997a).

Taking into account that the sensitivity of stem elongation to temperature is not the same during 24 h, to obtain a maximum effect on elongation control a shift in temperature should be given when the sensitivity of the stem elongation to temperature is highest (Erwin & Heins, 1995; Hansen *et al.*, 1996). The last part of the night or the first part of the day is considered the moment with especially high sensitivity of elongation rate to temperature (Myster & Moe, 1995). This is likely to be triggered by a 'light-on' signal, as the light perception is assumed to be an important component of the sensitivity response (Langton, 1998). The shift in temperature of a standard negative DIF treatment is commonly applied at daybreak (e.g. Bertram, 1992; Cockshull *et al.*, 1995; Langton & Cockshull, 1997a). However, it can also be done 2 h before sunrise in a greenhouse, without reducing the effectiveness of negative DIF in decreasing internode length of chrysanthemum (Jacobsen & Amsen, 1992). This is most likely the result of the fact that in this way the first hours of the day still have a low temperature, as Bertram (1992) found that 8°C temperature Drop for only 2 h before sunrise did not affect chrysanthemum stem elongation. Concerning the effectiveness of the DIF treatment it was found that:

- i. Absolute magnitude (i.e. value) and sign (i.e. + or -) of DIF were the critical factors determining final internode length (Carvalho *et al.*, 2002);
- ii. The response of internode elongation to DIF is greater when DIF increases from zero to positive values, than from negative values to zero (Moe, 1990; Heins & Erwin, 1990);
- iii. DIF has the greatest effect on plant height during the period of rapid growth in determinant crops (Heins & Erwin, 1990);
- iv. Furthermore, the responses to DIF are rapid, and most plants respond to a change in DT and NT within 24 h (Myster & Moe, 1995).

An alternative strategy to the standard DIF is the DROP treatment, i.e. a short-term temperature reduction with only a brief duration of temperature DROP, usually during the early part of the light period (e.g. Bertram 1992; Sach, 1995; Cockshull *et al.*, 1995; Hansen *et al.*, 1996). The effectiveness of DROP treatments in reducing stem length is related with its magnitude, duration and timing (Table 1). In general it increases consistently with the magnitude (2, 4 and 8 °C DROP) or duration (3 and 6 h) (Cockshull *et al.*, 1995). There is also a strong influence of the moment that a shift in temperature occurs (Bertram, 1992; Cockshull *et al.*, 1995). In agreement with the above mentioned strong temperature sensitivity of stem elongation in the early morning hours, Bertram (1992) found that 8 °C temperature DROP for 2 h before sunrise did not affect chrysanthemum stem elongation. However, Cockshull *et al.* (1995) observed a stronger effect of 3 h DROP treatment when applied 3 h after sunrise compared to directly following sunrise.

Table 1. Effectiveness of different DROP strategies (magnitude, duration and timing) in reducing internode length in chrysanthemum (Carvalho & Heuvelink, 2001).

Magnitude (°C)	Duration (h)	Timing	Photoperiod	Effectiveness	Authors
8	6	From sunrise	SD	+	Sach (1995)
2, 4 or 8	3 or 6	From sunrise and 3h after sunrise	SD	+	Cockshull <i>et al.</i> (1995)
12	2	From sunrise	SD	+	Hansen <i>et al.</i> (1996)
12	2	Different times of the day	LD	–	Hansen <i>et al.</i> (1996)
8	2	Before sunrise	SD	–	Bertram (1992)

Many authors report that the efficiency of DROP treatment, in reducing stem elongation, is often lower than the DIF treatment (Bertram, 1992; Cuijpers & Vogelesang, 1992; Hendriks & Ueber, 1995). The use of different cultivars (Hansen *et al.*, 1996) and an interaction between growth factors (Myser & Moe, 1995) are also possible reasons for differences in the effect of the temperature treatments. For instance, there is a higher sensitivity of length growth to temperature during the SD period, compared with LD (Myser & Moe, 1995). Several authors have shown this photo-period influence on the efficiency of negative DIF (Cuijpers & Vogelesang, 1992) and DROP treatment (Vogelesang *et al.*, 1992; Hansen *et al.*, 1996) in reducing internode length (Table 1). Moe & Heins (2000) presented a list of reasons that can explain poor responses to DIF and/or DROP regimes and can be the reason why the effects of DIF and temperature DROP on plant morphogenesis differ between research reports:

- The plant species in study has a small response to these temperature regimes;
- The cultivar under trial has a small elongation capacity (dwarf cultivars);
- Poor control of actual air temperature inside the greenhouse (e.g. lowering the greenhouse air temperature during the day is not possible due to high outside air temperature);
- Temperature DROP was too small or did not last long enough;
- DIF and/or DROP regimes started too late in the cultivation period;
- Interactions with growth conditions that enhance elongation (e.g. high plant density, far-red light, high N-supply).

2.1.2 Light intensity

Light intensity has a significant positive effect on stem elongation in several plant species. For instance, it was found in chrysanthemum, salvia and petunia that a higher irradiance during the day led to higher stem elongation rate (SER) during the following night, which resulted in longer stems (Bertram & Karlsen, 1994). However, based on different studies it is concluded that as long as a sufficient amount of assimilates is available for growth the effect of light intensity on elongation is relatively limited. Carvalho (2003) reported that increasing light intensity from 4.2 to 18.3 mol m⁻²d⁻¹ increased cut chrysanthemum plant height less than 10% (comparing plants growing in different seasons but under similar growth conditions). Moreover, as later pointed out by Carvalho *et al.* (2005) the light intensity effect on promoting stem growth can also be partly linked to a consequently higher plant temperature. A recent study conducted in *Kalanchoe blossfeldiana* was carried out in climate chambers, which allowed separating the effect of light intensity (60, 90, 140 and 200 µmol m⁻²s⁻¹ photosynthetic photon flux density, PPFD) from the effect of temperature (18, 21, 23 and 26°C; equal day and night temperature). Similarly to what was observed for chrysanthemum, light intensity only had a marginal effect on kalanchoe plant height, as increasing PPFD by more than a factor three (from the minimum to the maximum light level) plants became only 12% longer (Carvalho *et al.*, 2006). Our conclusion is also consistent with the observations in chrysanthemum that the use of supplementary light during daytime only resulted in longer plants at low natural irradiance levels (Hughes & Cockshull, 1972; Parups, 1978; Eng *et al.*, 1985). However, the way that stem elongation reacts to supplementary light may vary. On the one hand, supplementary light can enhance elongation (more assimilates available; Hydrangea (Verberkt, 1995a, Strauch, 1990), rose (Verberkt, 1997a), Codiaeum, Fatshedera, Hedera, Ficus and Schefflera (Verberkt & Vegter,

2007), on the other hand elongation can be reduced (HPS lamps have high R/Fr ratio (next paragraph); e.g. *Hibiscus rosasinensis* (Ludolph, 1990), *Spathiphyllum* and *Begonia* (Verberkt & Vegter, 2007).

2.1.3 Light quality (Red/Far-red ratio; Blue light)

It is well known that plant height is regulated by the action of phytochrome and blue light level. Increasing either the level of phytochrome photoequilibrium ($\phi = \text{Pfr}/\text{Ptotal}$ ratio: ratio of Pfr to total phytochrome) or the level of blue light (Khattak & Pearson, 1997; Oyaert *et al.*, 1999) decreases plant height (Heins & Wilkins, 1979). Thus, the use of red light (R-light) inhibits elongation and far-red light (FR-light) increases elongation through an induction response of phytochrome. Consequently a high R/Fr ratio will enhance axillary branching and reduce stem elongation, whereas a low R/Fr ratio will stimulate the apical dominance and therefore also stem elongation. Different types of lamps have a different R/Fr ratio (Table 2), and this must be taken into account when selecting lamps for supplementary lighting (see chapter 4.2). Another important aspect that shouldn't be neglected is that there is a natural variation in the light quality throughout the day. The R/Fr ratio decreases at the end of the day, which occurs naturally during twilight and it has been shown to increase the stem elongation in different species (Blom *et al.*, 1995; Blom & Kerec, 2003) comparable to the one observed in EOD-Fr treatments (Lund *et al.*, 2007). The duration of the twilight period depends on the season and latitude (longer in the summer and in the higher latitudes) (Lund *et al.*, 2007).

Table 2. Red far-red ratio (R/Fr) under different light sources (Spaargaren, 2000).

Light conditions	R/Fr ratio
Unclouded weather ^x	1.15
Incandescent light (light bulb)	0.72
High pressure sodium lamps	2.00
Fluorescent light (TL 84)	8.39

^x The Netherlands

A number of studies have examined whether the manipulation of spectral quality has potential for controlling stem elongation. Many attempts have been made to remove the elongation stimulus of FR-light from the natural spectrum, mostly using different photoselective screening materials. The 'fluid roof system' filter, with copper sulphate solutions (CuSO_4 liquid filters: high ϕ and high blue light transmission), was very efficient in reducing chrysanthemum plant height as it reduced SER, resulting in shorter internodes (e.g. Mortensen & Strømme, 1987; McMahon *et al.*, 1991; Rajapakse & Kelly, 1992; McMahon & Kelly, 1999). However, the magnitude of their effect depends on the chrysanthemum cultivar (Rajapakse *et al.*, 1993) and on the growing season (larger effect in spring and autumn compared to summer) (Rajapakse & Kelly, 1995). The effectiveness of CuSO_4 liquid filters in decreasing stem elongation was also confirmed for *Rosa hybrida* L. 'Meirutral' (McMahon & Kelly, 1990), *Lilium longiflorum* Thunb. 'Nellie White' (Bachman & McMahon, 1995), Poinsettia (McMahon & Kelly, 1990) and various bedding plant species (Benson, 1992). The effect of CuSO_4 filters can be explained by the increase in the R/FR ratio and blue/red (B/R) ratio of the transmitted light (Rajapakse & Kelly, 1992). In spite of being effective for a broad range of ornamentals these filters are not being used in practice (Hendriks & Ueber, 1995; Murakami *et al.*, 1997) because a liquid filter is difficult to apply on a greenhouse scale (Hendriks & Ueber, 1995; Oyaert *et al.*, 1999), requires double layered greenhouses which are very costly (Rajapakse *et al.*, 1999) and also due to the negative effect on total plant dry mass as a consequence of the strong reduction in the light intensity (Mortensen & Strømme, 1987; McMahon *et al.*, 1991; Hendriks & Ueber, 1995).

In the last decades light-weighted flexible plastic films have been engineered to selectively reflect a significant portion of Fr light without the practical limitations of the 'fluid roof system' (Clifford *et al.*, 2004). Oyaert *et al.* (1999)

evaluated the effect of different blue polyethylene (PE) films (low ϕ and high blue light transmission) on growth reduction of chrysanthemum plants, using different pigment concentrations. The inhibition of stem elongation increased with increasing pigment concentration, with a maximum of 22 % growth reduction. However, blue filters also decreased total plant dry mass (Oyaert *et al.*, 1999) due to lower light intensity of the transmitted light. The vaporised mica film is an alternative filter characterised by a higher light transmission capacity and higher R/FR ratio but a lower B/R ratio, compared to blue PE films (Oyaert *et al.*, 1999). Therefore, despite the rather small reduction in chrysanthemum stem elongation (9 %), Oyaert *et al.* (1999) suggested that the vaporising technique should be improved as this film has the advantage of reducing stem elongation without decreasing other plant quality aspects (no significant effect on branching rate, leaf area and plant dry mass).

Later studies were carried out with three photosensitive films that specifically reduce the transmission of Fr, B and R light in order to quantify their effect on the extension growth of poinsettia (Clifford *et al.*, 2004) and of five LD plants: *Campanula carpatica*, *Coreopsis* \times *grandiflora*, *Lobelia* \times *speciosa*, *Pisum sativum* and *Viola* \times *wittrockiana* (Runkle & Heins, 2001). Poinsettia plants grown in environments deficient in Fr light were about 20% shorter than control plants, whereas internode length was 9% and 71% greater in B or R light deficient environments, respectively. It was concluded that internode elongation in poinsettia is highly sensitive to the R/FR ratio but that negative effects on the time to final harvest were present (Clifford *et al.*, 2004). Similar findings were observed in the stem elongation of the above mentioned LD plants, where the Fr light deficient environment suppressed extension growth by 14 to 21% and both R light and B light deficient environments promoted extension growth by up to 65% and 100%, respectively (Runkle & Heins, 2001). Nevertheless, in some species of LD plants the Fr light deficient environments suppressed the flower initiation and development. To overcome this delay in flowering Runkle & Heins (2003) investigated the possibilities of exposing a LD plant (pansy) to periods of Fr light. This was done using incandescent lamps, but it was concluded that adding Fr light during the day or the night could only partly reduce the delay in flowering.

2.1.4 Photoperiod

Reduced duration of the LD period applied to short-day ornamentals with a determinate growth pattern is a frequently used method to achieve compact plants (Hendriks & Ueber, 1995; Heuvelink *et al.*, 1998; McMahon & Kelly, 1999). The stem length reduction is mainly a result of fewer internodes, due to earlier flower initiation (Heuvelink *et al.*, 1998), but also shorter internodes (Cathey, 1974). In chrysanthemum, when photoperiod extension is done during the natural SD period it was observed that the effect on stem elongation depends on the timing that the plant is exposed to light (night break lighting vs. morning or evening day extension). Given a night interruption of 4h, chrysanthemum showed a typical LD response (Cathey, 1974) resulting in longer internodes (Cathey, 1974) and taller plants (Cathey, 1974; McMahon & Kelly, 1999), than those lighted for the same duration but extending the photoperiod (Cathey, 1974). Moreover, internode length was considerably longer when chrysanthemum was exposed to light during the last 4 h of the dark period, rather than during the first 4 h (Cathey, 1974).

Another example of an effect of photoperiod on height is with petunia which can change its habit – often short compact rosette plants under short days, and single-stemmed and upright with little branching under long days (Steve Adams, pers.comm.). Trials carried out with *Calibrachoa* hybr. 'Red Million Bells' and *Scaevola saligna* 'Safir' showed that plants treated with extreme short day (6 h light, ESD) became more compact and developed a higher number of lateral shoots, as compared to plants grown at 8, 10 and 12 h photoperiod but with the same daily light integral (Schussler & Kosiba, 2006). Plants of both species were exposed to ESD for a different number of weeks (from 0 to 8) leading to the most compact plants in the treatment with the highest number of weeks in ESD. The more compact plants could be placed denser during the ESD-period (space saving) and ESD made it possible to time the bedding plants to a specific date. The number of floral shoots was significantly higher at anthesis. Unfortunately, plant weights are not reported. These authors concluded that ESD is a potential tool for timing, growth regulation and energy saving for several pot and bedding plants.

2.1.5 Relative humidity

There are only very few studies on the effect of the relative humidity (RH) on plant height, but in general RH seldom causes any direct effect on plant growth, as long as diseases do not appear (Mortensen, 2000). In chrysanthemum it was observed that shoot length was positively correlated with RH, at constant temperature (Mortensen, 1986b; Gislerød & Nelson, 1997). However, this effect was only significant after four weeks with high RH and when comparing rather extreme RH levels (95% compared to 55%) (Gislerød & Nelson, 1997). In a climate room experiment with two *Kalanchoe* cultivars ('Tenorio' en 'Anatole') the effect of two different RH levels during the day (40% or 60%) and one level during the night (80%), on the length of the plants was investigated at two constant temperatures (21 or 26°C; Eveleens *et al.*, 2007). RH did not affect *Kalanchoe* plant length. In contrast, it was reported in petunia that elongation growth is influenced by RH (Armitage & Kowalski, 1983).

2.1.6 CO₂ concentration

CO₂ enrichment promotes both stem elongation and stem diameter, but in chrysanthemum it was found a more dominant effect on the later (e.g. Lindstrøm, 1968; Mortensen & Moe, 1983; Eng *et al.*, 1985; Mortensen, 1986a). Increasing CO₂ concentration (300-900 $\mu\text{mol mol}^{-1}$) favoured stem mass over elongation, resulting in higher stem 'strength' (Heij & De Lint, 1987). However, above a certain CO₂ concentration (saturation level around 1000 $\mu\text{mol mol}^{-1}$) there are no further significant effects on chrysanthemum growth (Mortensen & Moe, 1983).

2.1.7 Plant density and pot size

Both plant density and pot size have an indirect effect on stem elongation as they influence the microclimate within the crop (Heins & Wilkins, 1979). Plant density strongly affects light intensity and light quality. Plants growing at high plant density form a leaf canopy which reduces light intensity and absorbs most of the R-light, while transmitting and reflecting most of the FR-light (Heins & Wilkins, 1979). For instance, roses growing in The Netherlands with 290 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at the top and 11 $\mu\text{mol m}^{-2} \text{s}^{-1}$ below the crop canopy, represented a R/Fr ratio of 1.23 and 0.13 at the top and below the canopy, respectively (Spaargaren, 2000). These reductions in light intensity and ϕ result in taller plants (Heins & Wilkins, 1979) and this response is named 'shade avoidance' effect. However, it was found that increasing plant density to very high values in a chrysanthemum crop (e.g. 83-125 plants m^{-2}) strongly reduced plant height (Huld & Andersson, 1997), especially during autumn and winter seasons (Langton *et al.*, 1999). These results can be explained by the low light penetration levels that combined with high amount of shaded leaves (acting as sinks) reduces growth rate.

Some studies have shown that larger pots resulted in taller plants both in alstroemeria and in chrysanthemum (Healy & Klick, 1993; Brum *et al.*, 2007). However, Carvalho *et al.* (2008) observed that the positive effect of pot size on stem length of *kalanchoe* is due to a higher number of internodes, which in turn is a consequence of the cultivation techniques and not a pot size effect per se. For instance, *kalanchoe* plants grown in larger pots had more internodes at harvest because of a higher initial number of internodes and because these plants were also subjected to a longer duration of the LD period. These are common commercial practices for producing taller plants in bigger pots. On the other hand, in conditions of limited water availability it is likely that plants in smaller pots will be more vulnerable to water stress resulting in shorter internodes.

2.1.8 Relevant interactions between climate conditions

Identifying the interactions between growth conditions is important both for the development of methods to control plant height and for further progress in the understanding of the physiological mechanisms behind the internode elongation process (Grindal *et al.*, 2000a). Most of the interactions described in literature are related to light (intensity, quality or photoperiod) affecting the effectiveness of the DIF or DROP treatments in controlling stem elongation.

DIF/DROP and light intensity: Some studies have shown that stem elongation responses to DIF (Erwin & Heins, 1995) and to DROP (Mortensen & Moe, 1992b) are negligible at low irradiance levels. For instance, DROP treatments did not affect stem elongation in several pot plants and bedding plant species including *Begonia × hiemalis* when grown at $80 \mu\text{mol m}^{-2}\text{s}^{-1}$. The reasons for this are not fully understood but it is expected to be related to the lack of carbohydrates under low irradiance levels. This hypothesis is reinforced by the work of Schouten *et al.* (2002) who modelled internode elongation in chrysanthemum. These authors stated that a sufficient amount of ‘elongation requirements’ is needed to have elongation (e.g. carbohydrates; for details see Chapter 3). Thus, plants grown under quite low light intensities are already limited in terms of elongation and therefore no additional effect of DIF/DROP strategies can be observed.

DIF/DROP and light quality: Previous work has shown that thermomorphogenic responses caused by negative DIF are similar to the plant photomorphogenic responses caused by high R/FR ratio or by R light, resulting in reduced internode elongation (Moe & Heins, 1990), and both reduced growth similarly to the application of chemical growth retardants (Starman *et al.*, 1989). On the other hand, the responses of the plants to a low R/FR ratio or to FR enriched light are similar to the ones observed in plants grown under a positive DIF (Moe & Heins, 2000). However, a clear interaction between DIF and light quality has been demonstrated. Continuous FR light or incandescent light (low R/FR ratio) almost nullifies reduction in stem elongation resulting from negative DIF in *Campanula* (Moe *et al.*, 1991), *Fuchsia* (Erwin & Heins, 1995), and pea (Grindal, 1997). In *Campanula isophylla* it was observed that day extension with incandescent lamps eliminated the negative DIF response, whereas with fluorescent lamps (high R/FR ratio) the response to the negative DIF was enhanced (Moe *et al.*, 1991; Mortensen & Moe, 1992b). A 30 minutes end-of-day (EOD) FR treatment was also effective in decreasing the inhibitory effect of the negative DIF (Moe & Heins, 2000). The manipulation of the light quality using selective plastic films also interacted with DIF in a similar way as described above for supplementary lighting (i.e. based on the R/FR ratio). However, the effect of the blue light on plant responses to DIF is not well known (Moe & Heins, 2000). A preliminary study with *Fuchsia* suggests that supplemental blue lighting during the day reduces elongation as compared to white light with the same R/FR ratio, but does not interact with DIF (Maas & Hattum, 1998).

DIF and photoperiod: The duration of the light period interacts with DIF to affect internode elongation. In general, longer photoperiods reduce the effectiveness of the DIF treatments. It has been shown that the reduction in stem length in pea plants grown under negative DIF, as compared to positive DIF, decreased from 44 to 30% as photoperiod increased from 10 to 14h (Grindal, 1997). Furthermore, it was found that many species that grow under natural long days during summer in Northern Europe, show less response to negative DIF than the same species when grown in the United States (Vogelezang *et al.*, 1992; Erwin & Heins, 1995). Differences in the effectiveness of the DIF treatment among locations are most likely due to a lower irradiation level or longer photoperiods observed in Northern Europe.

2.2 Growth conditions in the root environment

2.2.1 Nutrients (N, P, Ca)

The possibilities to produce compact floricultural crops by the regulation of nutrient supply were explored in several studies (e.g. Hansen & Petersen, 2004; Baas *et al.*, 1995; Dalal *et al.*, 2005). In general, nutrient supply in the cultivation of horticultural crops will be non-limiting for growth. However, if the nutrient supply is decreased below the critical concentration for maximum growth, it will be limiting for plant growth (Fig. 1). The way the plant responds to a limited supply of a nutrient will be determined by the function and mobility of that nutrient in the plant and by the properties of the plant. In general, the deficiency will first result in a growth decrease, and if more severe, visible deficiency symptoms will appear. If a compact plant is desired, nutrients that affect stem elongation are the most interesting. To identify which nutrient has the highest potential for decreasing stem elongation, the function of nutrients in plant growth and observed plant response should be evaluated (Appendix 2). Next to the effect on decreasing plant height, the nutrient manipulation should not lead to other undesired effects on plant growth and quality, such as leaf chlorosis, brown spots, decreased flowering or the senescence of leaf tips and/or margins.

In Appendix 2, in the description of visual deficiency symptoms of N, P and Ca, reduced or “stunted” growth is reported. This indicates that these nutrients might give the best possibilities to reduce plant height, on a theoretical basis. However, low N easily leads to leaf chlorosis, which is certainly unwanted.

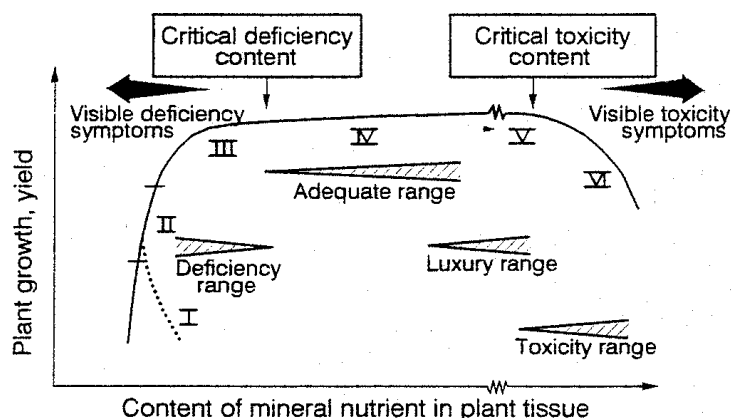


Figure 1. Effect of nutrient concentration on plant growth (source: Marschner, 1995).

The effect of the supply of a range of nutrients on plant growth was studied in many ornamental plants, such as Phalaenopsis (Yoneda *et al.*, 1997), Narcissus (Ruamrungsri *et al.*, 1996), chrysanthemum (Kageyama *et al.*, 1992, 1995), Hibiscus (Egilla & Davies, 1995), carnation (Medina, 1992), poinsettia (Albrecht *et al.*, 1992; Dale *et al.*, 1990), cyclamen (Hendriksen & Scharpf, 1985), primula (Mortensen & Holcomb, 1984) and Begonia, ficus, Hibiscus and Saintpaulia (Molitor *et al.*, 1984). However, the measurements are often restricted to plant fresh weight and quality characteristics, such as leaf colour and inflorescence. Plant height or internode elongation are often not reported. Pitchay (2002) studied the effect of reduced inputs of several nutrients on fresh weight of a large list of pot plants, but the effects on plant height were only conducted in Vinca (Figure 2). It was found that low inputs of almost all nutrients (except S) reduced plant height in Vinca, with respect to a control treatment with optimal nutrient supply. However, the largest reductions in plant height were caused by a suboptimal N and K supply. Deficiency symptoms of N included lighter green lower leaves, fewer and smaller leaves, a shorter plant and a reduced plant mass. The risk of reduction of quality is also mentioned by Ueber (1991) and Beel (1988). Beel (1988) found that a low level of N in Azalea showed reduction of growth, but also unexpected chlorosis of the younger leaves. Deficiency of K began with darker green foliage over the entire plant and a slower growth of leaves and internodes, resulting in a compact plant. Phosphorus deficiency resulted in darker green and shorter plants with smaller leaves.

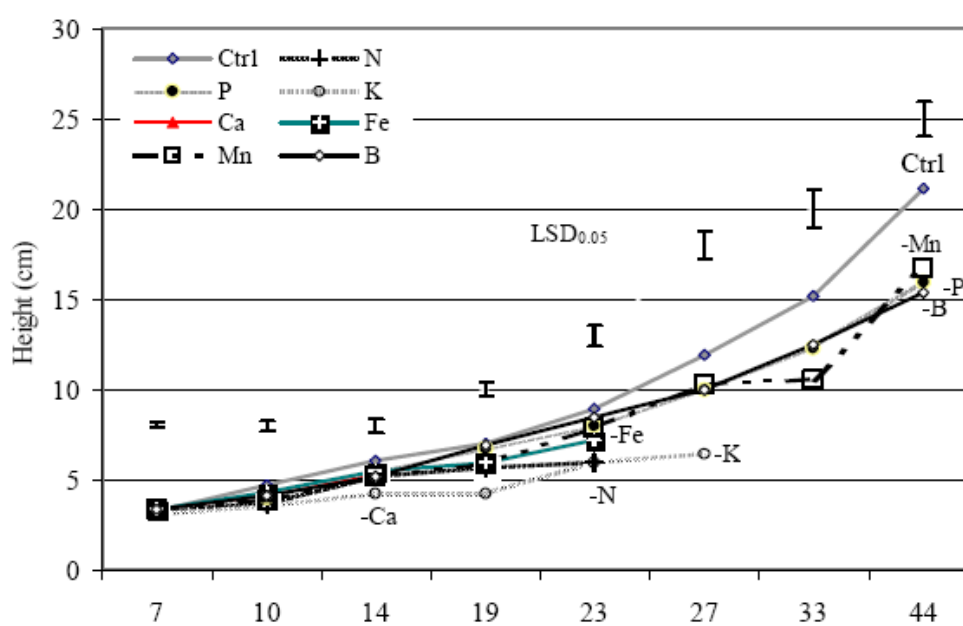


Figure 2. The effect of a reduced supply of several nutrients on height increase of *Vinca* (source: Pitchay, 2002).

Lewis *et al.* (1994) studied the effects of N, P and K supply on growth (in terms of shoot dry weight, stem elongation and inflorescence number and size) of *Limonium perigrinum* "Ballerina Rose". They concluded that the greatest response was to N, and P and K supply appeared to be less important.

Although the production of compact plants through the regulation of nutrient supply seems to be possible with several nutrients (especially with N, P and K) most recent research studies appear to be focused on P (e.g. Hansen & Petersen, 2004; Hansen *et al.*, 2005; Baas *et al.*, 1995; Dalal *et al.*, 2005; Warmenhoven, 2003), sometimes in combination with N (e.g. Hansen & Petersen, 2004; Hansen *et al.*, 2005). The reason for the choice of P as the most appropriate nutrient to regulate plant height is not fully clear, but it might have to do with the combination of the desired effect of P on plant height and the smaller risk of undesired effects of P on plant quality, such as yellowing or necrosis of leaves.

Plants take up more phosphate than strictly required for growth and metabolism. A low phosphate level suppresses shoot growth, increases carbon allocation to the roots and decreases the shoot/root ratio so that the plant is better able to cope with stress; water and nutrient uptake improve under less favourable conditions. Suppressed shoot growth results from less photosynthesis and higher root respiration. Low phosphate can change source/sink relationships. Increased root activity can be induced without reduction of the biomass by using lower phosphate levels or by using buffered phosphate and in combination with higher CO₂ levels, shelf life can be improved (Borch, 1997; Hansen *et al.* 1998).

Reduced amount of phosphate in the nutrient solution is an alternative method for chemical growth regulation in summer flowering bedding plants such as *Petunia* and *Pelargonium* but it can delay plant development and decrease the number of side shoots. Phosphate deficiency in *Pelargonium* caused a pronounced leaf marking which was caused by extra anthocyanin production often associated with low phosphate levels (Baas, 1991). Baas (1991) studied low phosphate and concluded that the best treatment was 0.4 mg/l P in the potting compost mix and 0.06 mmol/l P in the nutrient solution. Research on low phosphate in flowering bedding plants showed a clear reduction in the length in *Ageratum*, *Antirrhinum*, *Begonia*, *Geranium*, *Lobelia*, *Impatiens*, *Petunia* and pansy with 0.3 mmol/l P (Bragg & Fuller, 1997). Reduction in length was, in some cases, up to 90% but this resulted in reduction of quality.

A considerable amount of research on the influence of phosphate on growth has been conducted in Denmark. The shoot length in pot roses can be reduced without influencing root growth and plant quality. Only extreme phosphate deficiency reduces the photosynthesis. The levels used in this research were 0.005, 0.05 and 0.5 mmol/l P (Nielsen 1998). Other pot rose research (Hansen & Nielsen, 2001) showed that a reduction of phosphate level by 90% (from 0.5 to 0.050 mmol/l P) reduced shoot length by 30% without loss of quality. Hansen & Peterson (2004) reported that low N reduced plant height in *Hibiscus rosa-sinensis* by 21% and P by 15%, but they did not discuss effects on leaf colour.

Good quality compact flowering bedding plants propagated from cuttings such as Fuchsia, Osteospermum, Pelargonium en Petunia can be grown with 0.2 mmol/l P in the nutrient solution, without P in the potting compost mix and low levels of growth retardants (two treatments during the cultivation with 2 g/l Alar 64 and 0.75 ml/l CCC). A phosphate level of 0.2 mmol/l is too low for the crops Verbena and Bacopa as Verbena develops necrotic leaf edges and Bacopa develops purple-coloured leaves. The quality of all the crops is good, except for Petunia that is still too tall, when 1 kg potting compost mix with reduced phosphate (NPK 15-4-30) is used. The reduction in height varied from 15 to 50% with little or no loss in quality such as less shoots, flowers or damaged leaves. The quality of flowering bedding plants propagated from seed such as Begonia, Impatiens, Lobelia, Petunia, Tagetes and Verbena is not good enough when grown using 0.2 mmol/l P without potting compost mix with reduced phosphate. A phosphate level of 0.2 mmol/l in combination with 1 kg NPK 15-4-30 per m³ potting compost mix is sufficient to obtain a good quality but only when the crop has been treated 1-3 times with 4 g/l Alar 64 and 0.3 ml/l CCC (Warmenhoven *et al.*, 2005). By intensive measurements on the soluble phosphate and the stock phosphate it is possible to use a very low phosphate dose and grow a good quality crop (T. Dijkstra, pers. comm.).

In 2007 the optimum ratio between nitrogen and potassium in the nutrient solution and the substrate when the phosphate level is low, was investigated so that the reduced phosphate level could be effectively used to regulate growth. This research on Pelargonium and Petunia from cuttings and Petunia and Verbena from seed concluded that with all the species from cuttings or seed the phosphate level was too low at concentrations of 0.1 or 0.2 mmol/l P in the nutrient solution without phosphate in the potting compost mix. This was especially visible for the start of the development of the shoots. A potting compost mix for Petunia is not necessary because the nutrient levels here can be quickly adjusted and the phosphate level in the nutrient solution need not be higher than 0.2 mmol/l P, certainly not when a compact plant must be grown. The phosphate levels do not have any effect on the uptake of the other nutrients because no differences in the concentrations of these elements were found in the plants when only the phosphate levels differed (Warmenhoven & Van Noort, 2007).

Reduction of the phosphate level (from 0.35 to 0.14 mmol/l) in Begonia, Poinsettia and Pelargonium causes no problems. In Poinsettia this concentration causes a growth reduction (Grantzau, 2006) which was already observed also by Straver (1994). In this research 0.25 mmol P resulted in a reduced plant height but had no effect on the quality, whereas lower levels of 0.05 and 0.10 mmol P/l did have a negative effect. Pot chrysanthemum showed growth reduction only at extremely low phosphate levels and this had an immediate effect on the quality because the plant became too 'spiky' (Van Leeuwen, 1992). Hydrangea showed not only growth retardation when the phosphate levels in the compost and/or the nutrient solution were reduced but also less shoot development and fewer and smaller flowers during forcing (Van Leeuwen, 1994 en 1995).

German research on phosphate in Hydrangea showed that a reduction in height without a large reduction in numbers and quality of the flowering heads could be achieved by adjusting the phosphate level to the crop stage. This was done by varying the phosphate levels in the nutrient solution, no phosphate during the growth but sufficient phosphate at the start of the crop and during shoot development. The result was a 25% reduction in height without much loss of quality in number of heads, size of the heads and leaf quality (Richter, 2004a,b). In The Netherlands, dynamic phosphate application in Hydrangea has also been used in practice. 5% P₂O₅ was added to the potting soil mix and then extra P₂O₅ was only added three times around the last pruning stage and bud initiation (Dijkstra, 2007).

2.2.2 Compalox

In addition to a direct regulation of P supply by the fertilization regime, the P availability in the growing medium may also be affected by more indirect measures. Examples of indirect measures that affect P availability in potting soils are the use of a P buffer (e.g. Compalox, that exists of aluminium oxide) and clay (that may contain iron and/or aluminium (hydr)oxides). Warmenhoven (2003) studied the effect of Compalox and clay in primula. She concluded that Compalox and clay reduced growth and development, but an explanation for this was not given. Most probably, the effect of Compalox can be explained by the effect on the P concentration in the nutrient solution, while the effect of clay might be explained by a combination of chemical (among others a lower P concentration) and physical properties of the growing medium. The P that is adsorbed by Compalox and/or clay may become available for plant uptake by desorption (Fig. 3).

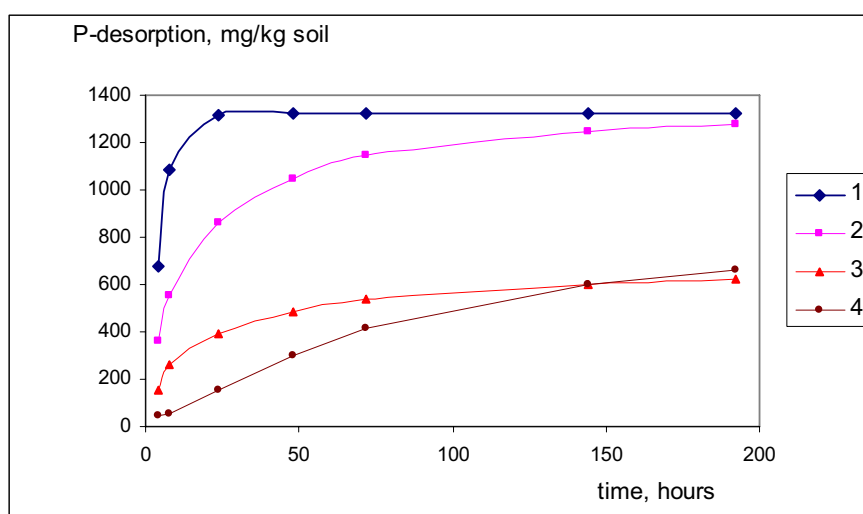


Figure 3. *P*-desorption behaviour in fertilized peat (trt. 1), peat with 15 kg clay per m³ peat (trt. 2), peat with 60 kg clay per m³ peat (trt. 3), peat with 5 kg Compalox per m³ peat (trt. 4). Results of laboratory experiment in which P is continuously removed from soil solution (unpublished results).

Compalox-P-buffer is an activated aluminium oxide (Al₂O₃) including an amount of bonded phosphate. This product binds phosphate at high phosphate concentrations and releases phosphate when the phosphate concentration decreases. When this buffer is mixed into the substrate a stable phosphate concentration can be maintained. This phosphate buffer makes it easier to grow crops at a low phosphate concentration without the occurrence of deficiency symptoms. For effective use 1% of this buffer must be mixed through a medium and Compalox must be the only source of phosphate (Jagers op Akkerhuis, 2002). Potted sunflower plants do show a slight but insufficient growth reduction when grown under low phosphate (in combination with and without Compalox) and this is more when the phosphate is reduced more. This effect is detrimental for the quality (Ueber, 2001; Ueber, Maseman, 2002). Research on flowering bedding plants showed that Compalox differs in effect in different species and even within one species the effects are not always the same. Compalox 2% (20 g/l) works well in Anagallis, Fuchsia and Verbena 'tukana', but has no effect on Osteospermum, Petunia, Scaevola and Verbena temari (Neumaier, Röber, 2003). Research on Hydrangea showed that Compalox gave no useful reduction in height (Richter, 2004a,b). In Solanum, research showed that at very low levels Compalox gives a reduction in growth, not in height but on the size of the leaves and it causes yellowing of the leaf. Supplying more Compalox or phosphate than in the advice causes no growth reduction (Krijger, 2004).

2.2.3 EC and water availability

The salt concentration (electrical conductivity, EC) influences the water uptake of the roots. Increasing salt concentration makes water uptake more difficult and this reduces root growth. In reaction to this the shoot growth will also become affected and this is caused by a general lack of water in the whole plant. The effect of EC on stem length depends on the species and on the irrigation levels. In Pelargonium a high EC (3.0) reduced the length by 10% under normal irrigation levels (Van Leeuwen, 1992). However, high EC levels in a relatively well-watered crop had virtually no effect on the height of bedding plants, Pelargonium and Petunia (Graaf-Van der Zande, 1986). Therefore, often a combination of high EC and a drier cultivation strategy is used. Higher EC levels gave clear effects on the height of Impatiens New Guinea and pot chrysanthemum. Increase of the EC from 1 to 4 dS m⁻¹ reduced the height in Impatiens by up to 50% depending on the cultivar and resulted in more intense colored leaves although these were smaller and bobbled. The greatest disadvantage was the increase in the occurrence of leaf burning (Verberkt, 1993). In pot chrysanthemum a high EC (3.4 dS m⁻¹) gave a more compact plant with a lower fresh weight and shorter side shoots than an EC of 2.2 or 1.0 dS m⁻¹. Flowering was also a week earlier (Verberkt, 1996; De Beer, 2000). In contrast, EC had almost no influence on the development of height in Kalanchoe (Verberkt, 1996). In a recent experiment with EC in combination with changes in relative humidity (RH) the effect of EC on the elongation of the flowering shoots was again shown to be small (Eveleens *et al.*, 2007). Increasing EC level of the irrigation water from 0.6 to 2.2 dS m⁻¹ has no significant effect on growth and flowering during and after culture of Impatiens and Petunia (Mulderij, 1998).

Growth regulation with water deficit stress is commonly used and is an important tool for producing compact plants in a number of bedding plants and pot plants. Water stress results in different physiological responses, for example as leaf water potential begins to decrease, leaf enlargement is inhibited, whereas leaf photosynthesis and respiration are not yet affected. The decrease in leaf enlargement can result in less K uptake and that can give reduction in cell expansion. Severe water deficits result in yellow and damaged leaves (Liptay *et al.*, 1998). There has been research with limited water and an example is research where the fresh weight of Pelargonium was reduced by 60% by reducing irrigation by 40% during the whole cropping period (Hendriks, 2000). In Hibiscus is found that only drought the plant height reduced with 32%, it also reduces internode length, leaf area, fresh weight and amount of flower buds (Hanssen & Petersen, 2004). There also been research in Poinsettia, the conclusion was that limited water consumption can control height without losing quality. 50% less water gave 40% reduced height without problems with quality (Röber & Horn, 1993). The biggest problem is the risk of heterogeneity in growth, leaf scorching and reduction of quality (Hendriks, 2000; Gessnitzer, 1997).

2.2.4 Substrate (use of clay)

The effects of the addition of several clay products on the growth of Begonia (pilot crop) and on the physical and chemical properties of the growing medium were studied by Wever *et al.* (2004). The clay products tested varied in ion exchangeability and size of their particles. Adding a small amount of clay (100 g/l substrate) in combination with limiting the amount of water led to a small reduction of the plant height (3%) and also to a better shelf life. Wever *et al.* (2004) described the effects of adding a small amount of clay on the properties of potting soil:

Physical properties

- a decrease in the water binding capacity and the amount of water that is easily available to plants, which will cause relatively soon water stress.
- an improvement of the rewetting capacity of the potting soil by the clay additions, which will be favourable in ebb and flood systems. Wever *et al.* (2004) included different clays in their study, of which the size distribution of clay granules varied. The positive effect on rewetting was the biggest with the finest clays.

Chemical properties

- cation exchange capacity is increased, the concentrations of the cations K and NH₄ in the soil solution are decreased and the concentrations of Ca and Mg in the soil solution are increased compared to the potting soil without clay. Differences between the clays included in the study could be explained by differences in soil texture (especially the amount of clay particles < 2 µm) and differences in the type of clay minerals (smectite, vermiculite, kaolinite, illite). The resulted effects on the cation concentration in the soil solution may affect plant growth.
- P concentration in the soil solution was reduced by clay addition to the potting soil. As has been mentioned before, this effect may be ascribed to P adsorption by iron and/or aluminium (hydr)oxides. The effect was found with all clays, but the effect differed between clays, due to differences in its content of iron- and/or aluminium(hydr)oxides. The reduction in the P concentration in the soil solution may also affect plant growth.

2.3 Stress factors (mechanical stress, cold water application)

The negative effect of mechanical stress (thigmotrophy) by regular touching or brushing the plants on plant height has been well-known for many years. The reasons behind this effect are probably related to the fact that during any mechanical stress the plant produces a very small amount of the natural growth regulator ethylene, resulting in shorter and stronger plants. The vegetative growing tip reacts the most to this sort of treatment. This could mean that contact and shaking stress should be administered in the vegetative phase and that after transition to the generative phase another method is more suitable. Air movement had a slight effect in *Hydrangea*, but no effect on *Osteospermum*. The fast senescence of the plants was an important disadvantage. Ultrasound had an effect on *Hydrangea* (4.5%) and on *Osteospermum* (11.2%), however the number of flowers in the *Osteospermum* was clearly reduced.

Research has mainly been done on *Impatiens*, *Petunia*, pansy, *Poinsettia*, pot chrysanthemum and on young plants of tomato, sweet pepper and cucumber. In the glasshouse vegetables it was possible to use contact stress in the propagation stage as a growth control method to obtain strong and short plants. The length of the contact period seemed to be more important than the number of times the plant was touched. In pansy it was found that 10 to 20 brushes per day, 5 days a week gave 25-30% less elongation without damage or a delay in growth. In *Pelargonium* and *Petunia* the brushing had no effect. There was an effect in *Impatiens*, but it gave too much damage (Garner, 1997). In Germany research was done on the effect of brushing the plants with pieces of fabric and in pot chrysanthemum this gave 6% less growth compared to 8% under drought stress, but the number of buds and flowers in the brushing treatment was higher (Gugenhan, 1999). *Osteospermum* and *Hydrangea* both reacted considerably to shaking (*Osteospermum* approx. 29% reduction, *Hydrangea* approx. 10%). Brushing also gave a considerable effect in *Hydrangea* approx. 8% but the flower heads were smaller in (12%). *Osteospermum* did not react to brushing. With *Geranium* and *Impatiens* shaking gives delay of flowering, but Pansy had no delay of flowering (Cipollini, 1999.)

Although a clear effect on growth was shown and brushing caused a reduction of height, this method has hardly been used on a large scale because many foreign nurseries have a low level of mechanisation and the application of an automatic brushing system is therefore difficult. Also the effect achieved by this method was much less than that of chemical growth retardants (*Poinsettia*: 10% reduction compared to 25-50% reduction using chemical control). Additionally many growers were uncertain about this method because of other possible adverse effects like leaf damage.

Several papers show that sprinkling of the growing tips with cold water can reduce the height of *Impatiens*, *Lycopersicum* (tomato) and *Lilium*. In *Heliotropium* and *Solanum*, the reduction in stem elongation was too small for practical purposes (Chen *et al.*, 2001; Blom & Kerec, 2004; Krijger, 2004). It seems that cold water influences the gibberellin metabolism, but not the sensitivity to ethylene, because use in combination with silver-thiosulphate

(ethylene inhibitor) had no effect. The use of cold water for growth control has a few practical disadvantages such as the timing of the treatment, the amount of water required, EC reduction and the incidence of fungal infections.

2.4 Plant growth regulators

Plant growth regulators are organic compounds that promote or inhibit the physiological processes in the plant. The regulators can be divided in two groups: the natural growth regulators (plant hormones) and the chemical growth retardants. Natural growth regulators are hormones produced by the plant itself in a particular organ and further transported to other locations within the plant where they will be involved in a given process (e.g. flowering, dormancy etc). These physiological processes are dependent on the concentration of individual hormones and on the balance between different hormones. Chemical growth retardants imitate or influence the natural growth regulators, e.g. rooting hormones (imitating auxins), flower-induction hormones (imitating ethylene, e.g. in Bromeliaceae), synthetic gibberellins with influence on growth and flowering (*Spathiphyllum*) and growth retardants like Daminozide and Chlormequat to produce compact plants.

2.4.1 Plant hormones

Plant hormones are signal molecules, which in small tissue concentrations trigger physiological responses. Most plant hormones have multiple effects on plant growth and development and several of them seem to be involved in regulating elongation growth. This is the case of the hormones listed below.

Gibberellins (GAs)

Gibberellins originate in all young plant parts and in seeds. Transport probably takes place via the phloem and xylem. GA forms a family of currently 126 compounds identified in plants, fungi and bacteria. However, only a few of them are shown to be biologically active per se (Grindal *et al.*, 2000a). Gibberellins affect shoot growth and elongation through cell division and cell elongation. Gibberellin A1 (GA1) seems to be the main bioactive GA for stem elongation in most species studied (Appendix 3). The GA are named GA1 ... GAn in order of discovery. These plant hormones are known to regulate growth and influence various developmental processes including stem elongation.

Auxin (IAA)

Auxin is formed in leaf primordia, young leaves and in developing seeds. The transport takes place from cell to cell via the phloem and is also transported to the roots. Auxin affects cell division and differentiation, cell growth, shoot growth, root development, apical dominance (stimulation/inhibition of side shoot development) and high auxin concentrations induce ethylene formation. Auxins can be of natural or synthetic composition but they are not directly used for the growth of compact plants.

Cytokinins

Cytokinins originate from root tips, developing seeds and probably axial buds and are transported from the roots via the xylem to the developing shoots. Cytokinins affect the cell division, shoot development, axial bud development, leaf cell enlargement and elongation of the leaf, delay in leaf senescence, stomatal opening, development of chlorophyll and most likely the partitioning of assimilates. Factors that influence the root formation such as low temperatures, water stress, oxygen deficiency by lowering the cytokinin level also have an effect on the above-ground development of the plant. In general cytokinins are not used to regulate plant growth. In The Netherlands the use of synthetic cytokinins in horticulture is prohibited. Benzyladenine (BA) is a synthetic cytokinin used in some countries to stimulate shoot production in plants (e.g. *Dieffenbachia* hybrids, *Perperomia*) that do not branch easily. A reduction in BA concentration decreases the number shoots while at the same time reducing the height (Henny, 1986). It seems that the division of the assimilates between more shoots leads to a reduction in length.

Absciscic acid (ABA)

ABA originates in ripe leaves and in the roots, especially after water stress. Transport occurs via the phloem to the leaves and probably back to the roots via the xylem. The hormone ABA breaks the growth of young tissue and increases destruction and aging of older tissue. In young tissue ABA inhibits the effect of auxine and with aging of the tissue ABA inhibits the effect of cytokinine. ABA affects the closure of the stomata under water stress, transport of sugars to young seeds; whereas GA has a negative effect on these enzymes and inhibits development, ABA has an antagonistic effect to GA. ABA also inhibits GA-induced enzyme production and ABA promotes root growth and inhibits shoot growth at low water potentials (Taiz & Zeiger, 2002).

Ethylene

Ethylene (C₂H₄) is a gaseous hydrocarbon that is synthesized in many locations in the plant, mostly after stress situations, and it spreads by diffusion through the intercellular spaces. Ethylene has an effect on: the origin of adventive roots, aerenchyma (air canals) in roots, the abscission layer and it inhibits the development of young cells, stimulates senescence of mature tissue, stimulates flowering (Bromeliaceae), stimulates flower autocatalytic and stimulates its own production. In outdoor crops, wind causes a stress effect and stimulates flower opening and leaf senescence, whereas elongation of plants is reduced. Once ethylene is present in plant tissues it has an effect on ethylene production (autocatalytic process) and therefore also on the plant height. Ethylene affects the orientation of the cell wall fibres so that instead of cell elongation in a lengthwise direction the cells become wider.

Brassins or Brassinosteroid

Brassins are a group of steroidal plant hormones, that were first isolated from brassica pollen. These compounds promote vascular differentiation, stem elongation (cell expansion) and inhibit root growth and development. They are necessary for pollen elongation for pollen tube formation.

2.4.2 Chemical growth retardants

Chemical plant growth retardants (PGR) are mainly active in the meristems and in parts of the plant where growth occurs, reducing the cell elongation of those organs. High concentrations also inhibit cell division in the meristems. Reduction of cell elongation by these retardants is caused by inhibiting or reducing the synthesis of gibberellins, because this is the hormone that causes cell elongation resulting in stem growth. The effect of PGR depends on developmental stage, season, plant density and the condition of the plant, as well as on their concentration and method of application. A young plant grows quicker than an old plant and therefore it requires a more effective treatment. The season is also important and in the spring and summer a plant will need a more effective treatment than in the winter. Plants do not elongate at a constant rate and this rate depends on the developmental stage so it is important to know when plants elongate quickly and when there is little or no elongation. Low temperature gives less elongation than a higher temperature, a lower density also gives less elongation and this must also be taken into account when treating the plants (Kromwijk, 2001). A number of crops clearly show that the application of growth retardants on the cutting, immediately after pinching and/or early during the vegetative stage has a much larger effect than later on in the crop, e.g. *Acalypha*, *Hibiscus* (Herman, 1967), *Euphorbia p.* (Kromwijk, 2001), pot chrysanthemum (De Beer, 2000). Crop planning strategies have been developed for a number of crops, e.g. *Fuchsia*, *Kalanchoë*, *Pelargonium*, *Poinsettia* and pot chrysanthemum. In these strategies the normal plant growth without growth control is compared to the growth with growth control and these growth curves are the basis for growth and development. For example the height of the plants is recorded and using the growth curves the optimal point in time is chosen for a growth control treatment. This can help to reduce the amount of retardant used in the crop. One step further is the development of a growth model where the influence of light and temperature is known and growth control treatment can be based on this information (Kromwijk, 2002, 2005; Verberkt, 1998, 1999, 2001).

Application

Growth retardants can be applied by spraying, watering and/or soaking. When spraying a fine mist should be used for an even distribution. When watering and/or soaking, the plant must be able to take-up and use the solution through the roots. The disadvantage of watering or soaking is the extra time required for application.

The concentration of growth retardant is extremely important because there is often an optimum concentration for a process and therefore too high or too low concentrations will have a less favourable effect.

- The plants must be healthy and the pot soil must be damp because up-take of these substances is improved under these conditions and there is less chance of scorching. The plant must be dry because the substance must not be diluted nor drip off of the plant.
- The RH must be higher than 60% because otherwise the solution will evaporate too quickly.
- The optimal temperature for application is 18-21°C, but the temperature must not fall below 16°C nor exceed 25°C, because otherwise damage can occur or evaporation is so high that the substance is no longer effective.
- Spraying should not be carried out in direct sunlight as this is disadvantageous for up-take and it can stimulate scorching.

Damage

Damage can be caused by the type of substance, the concentration can be too high, the application frequency can be too high, the plant may be not healthy, interactions may occur with other substances that have been used, unfavourable climate conditions may exist. Damage is visible as chlorosis of leaf edges and/or damaged and dead areas on the leaf edges especially by young plants three to ten days after treatment. Low temperatures in combination with growth retardants can result in curling or malformation of leaves. Root damage can occur in combination with a high EC and/or high chloride levels.

Chlormequat (CCC)

Chlormequat reduces or completely blocks gibberellin production in plants (Appendix 4). Application of chlormequat results in smaller internodes and thicker stems making the plants more compact. A side-effect of CCC is a decrease in susceptibility to water stress, salt stress, temperature stress, nematodes, disease and pests. CCC can result in earlier flowering and darker leaves and enters the plant through the roots and leaves, although it is faster through the roots. The advantage of application via the roots is that less damage occurs making CCC suitable for a wider range of varieties. Additionally the substance remains more stable in the soil and it remains active for a longer period. CCC is only active for a short period in the plant and for a large number of plant varieties it is advisable to repeat a treatment after 10-14 days. CCC is broken down quickly in wet soil but not so quickly as in the plant. CCC is applied by spraying, watering or soaking and the effect is better if the crop remains wet for a certain time and if application occurs before sunrise or after sunset. Dosage is 2-6 g active ingredient per liter depending on the previous comments. More applications with a lower dosage are preferable to one application with a high dosage because of possible damage. When watering 8-10 g/l with 3 liter per m² is used. The substance is less effective under high temperatures (>25°C) and can react with metals during storage. In *Pelargonium* CCC can give a reduction in height of more than 30% (Armitage 1984). Other crops in which CCC effective is, are *Abutilon*, *Acalypha*, *Aphelandra*, *chrysanthemum* and *Hibiscus*, sprayed with a dosage of 0.15%-0.5% or soaked in 0.25-1.0% (Herman, 1967).

Daminozide (Alar)

Daminozide gives shorter internodes, but has no influence on the number of leaves or the leaf area. This substance works as an anti-gibberellin and as an anti-ethylene. In the latter case this means a delay in the ripening and therefore the flowering. The effectiveness remains in pot plants for 3-6 weeks and in woody shrubs this can be several months. This substance causes darker leaves because of a concentration of the chlorophyll. Daminozide enters the plant through the leaves and the roots and because it does not enter the plants through the stomata it is independent of light. Most of the substance enters the plant within the first 3-4 hours and it is important that the crop remains wet during this period. Daminozide works on a local systemic basis, having a very slow systemic

effect. It only works on parts of the plant where it is applied. Watering and soaking are therefore not so suitable and a single application has less effect. Two applications of half of the concentration are more effective than one application of the whole concentration and for a gradual effect Alar can be applied regularly. The concentration is normally between 0.5-3 g active ingredient and normally no surfactant is used. Daminozide reacts with metals and has no effect on monocotyledons but is effective on nearly all dicotyledons. The half-life of Alar in the soil is 21-28 days. Daminozide is used on Impatiens achieving a reduction in length of 12% and on Petunia values of 36% have been reached (Armitage, 1984).

Paclobutrazol (Bonzi)

Paclobutrazol strongly inhibits the development of shoot length and leaf area. Earlier flowering and extra flowering are also possible. Paclobutrazol is blocking gibberellin production (Appendix 4). This substance works better on young plants than on older plants. The ABA-level and IAA-level are reduced, while the cytokinin level is increased without extra shoot development. Treatment with this substance improves resistance to water stress and mildew and reduces the population density of insects. Paclobutrazol enters the plant through young tissues, roots and leaves and within 30 minutes it is present in the plant. After entering the plant it is transported through the xylem to the growing tips/meristems. Application is carried out by spraying, watering or soaking the plants but to achieve a homogenous treatment the suspension must be continually stirred. Concentrations that are too high can cause a long lasting growth inhibition of even a complete growth standstill in sensitive crops. Care should be taken as paclobutrazol is persistent in substrates, matting etc. (half life in the soil is 6 months to a year) and could therefore have consequences for subsequent crops. Bonzi can be used in combination with other growth retardants and in particular on crops that require considerable growth control.

Propiconazole

Propiconazole is a systemic fungicide from the triazole group and it blocks the working of gibberellin. Propiconazole has crop growth control properties and these depend on the dose, application frequency, crop stage, climate conditions and type of crop. The half-life of this chemical in substrate and surface water is 30-112 days. Propiconazole is used in nearly all the crops that are treated with growth control agents. The normal concentration lies between 0.05-0.1%. Propiconazole gave very good results for growth control in Primula, the diameter was reduced by 14% without showing any damage and less retardant was required when compared to other chemicals and/or combinations of chemicals suitable for growth control. Propiconazole has also been used in Hydrangea, both outdoors and in the greenhouse with reasonable results when compared to Daminozide, that has a more homogenous effect but requires much more retardant. Propiconazole can cause leaf malformation in Hydrangea (Lörcks *et al.*, 2004).

Adjuvants

Applied research showed that addition of the adjuvant ATplus UCL 1007 (at 250g/100 liter) can reduce the daminozide requirement (300-450g/100 liter) by 50% in similar length chrysanthemum without flowering delay, a lower stem weight or crop damage (Anonymus, 2004). In Kalanchoë addition of ATplus did show damage (Dijkstra, 2007). In Poinsettia research it was shown that the adjuvant Elasto G5 (at 0.25%) allowed up to 75% less CCC requirement (Lukassen, 2006), or made CCC application 2.5 times more efficient (Verberkt, pers.comm.). Elasto G5 also seemed the best adjuvant in Hydrangea but then in combination with Daminozide (Dijkstra, 2007).

Interaction

One of the characteristics of plant hormones is their large range of effects. Therefore the effects of one hormone overlap the effects of another and different hormones influence the same process. These effects can be antagonistic (opposition), additive (combined effects is the same as the sum of the separate effects) and synergistic (the effect of two hormones working together is stronger than the sum of the separate effects). In bedding plants Daminozide and CCC are often used in combination. A mixture often works better because the different chemicals affect the plant in different ways. Another advantage is that a lower dose of the stronger CCC can be used. A

combination of retardants often used in the bedding plants *Fuchsia*, *Osteospermum*, *Petunia*, is 2 g/l Alar and 0.75 ml/l CCC. CCC for example inhibits the production of gibberellins, Daminozide also has this effect but blocks and destroys the gibberellins that are present in the plant. Additionally Alar inhibits the production of ethylene. Currently there is also research on adjuvants that improve the effects of retardants so that less active ingredient has to be used. (see previous Chapter).

The importance of growth control measures increases when assimilation lighting is used as lighting generally causes more elongation.

3 Underlying mechanisms behind internode elongation

Most of the literature available on the underlying physiological mechanisms related to the control of elongation growth is focused on the physiological background of DIF. Few studies have also been conducted to understand the physiological basis of the effect of light quality on stem elongation and its interaction with DIF. The role of gibberellins (GA) in the regulation of stem elongation will be especially emphasized as there is a clear evidence of the involvement of these hormones in mediating both thermomorphogenic and photomorphogenic responses in stem elongation.

3.1 Control of cell growth

Stem elongation is based on two basic cellular processes: cell division and cell expansion, in which the latter includes cell length and width. Cell division is mainly a function of the ADT. Lowering the ADT will slow down cell division, but this does not have an effect on final plant height at maturity (E. Runkle, pers. comm.). On the other hand, cell expansion seems to be a more complex process mainly driven by GAs, which in turn are strongly influenced by DIF and light quality. To better understand the elongation process, cell number and cell length were recorded in fully developed internodes of *Lilium* (Erwin *et al.*, 1994), *Campanula* (Strøm & Moe, 1997) and pea (Grindal, 1997) grown under different DIF regimes. These studies have demonstrated that plants grown at a negative DIF have a reduced stem elongation due to a decreased cellular elongation (as a result of both smaller cell length and smaller cell width) rather than due to a lower cell division (Erwin *et al.*, 1994; Myster & Moe, 1995; Bachman & McMahon, 2006). Cell elongation decreased linearly as DIF decreased from + 15 to - 15°C (Erwin *et al.*, 1994).

As mentioned above in the 'Relevant interactions between climate condition' (Chapter 2.1), thermomorphogenesis induced by the DIF/DROP treatments and photomorphogenesis induced by light quality are often similar. Both a negative DIF and a low Fr/R ratio reduce internode elongation primarily through reduced cell elongation and not cell division. However, the physiological basis of stem elongation responses to DIF and light quality seem not to be identical (Moe & Heins, 2000).

3.2 GA-metabolism

Exactly how GA promotes stem elongation is not completely clear, but it seems to be closely linked to the cellular elongation processes. It was reported for pea that GA changes the orientation of microtubules and cellulose microfibrils, making the cells swell more in length (Duckett & Lloyd, 1994). Another effect of GA is that the activity of xyloglucan endotransglycosylase, the enzyme that hydrolyses and then re-links hemicellulose, is increased, enhancing wall stretching in pea (Potter & Fry, 1993). According to Grindal *et al.* (2000a), the inhibition of the internode elongation in plants subjected to a negative DIF is clearly related to a lower content of the bioactive GA1 in the plant tissue. These findings are supported by many reports, where GA-quantification and/or GA-application were performed, and that indicated that these hormones were strongly involved in mediating thermoperiodic responses in stem elongation (Stavang *et al.*, 2006). For instance, GA-quantification experiments have shown that the endogenous bioactive GA content is lower in negative DIF treated plants as compared to zero or positive DIF treated plants of *Campanula isophylla* and *Fuchsia* (Tangerås, 1979; Grindal, 2000a). Also in bellflower it was found that temperature regimes that stimulate extension growth had a higher concentration of the physiologically active GA1 and its precursors GA19 and GA44 (Appendix 3). Reciprocal temperature regimes were accompanied by an increase in the inactive hydroxylated form of GA53, the precursor of GA44 (Jensen *et al.*, 1996). Furthermore, experiments where GA applications were performed showed that GA could overcome inhibition of stem elongation in negative DIF grown plants of *Campanula* (Moe, 1990), *Fuchsia* (Tangerås, 1979; Erwin, 1991), *Lilium* (Zieslin & Tsujita, 1988) and *Begonia* (Myster & Moe, 1995). Also in tomato plants grown for 14 days in contrasting day-night temperature

regimes the average stem length increased considerably following addition of exogenous GA₄+7, irrespective of the DIF regime applied and whether GA-deficient mutants or wild-type plants were used (Langton, 1998). Similarly, studies on various mutants in several plant species clearly indicate that GA is an essential factor for normal stem elongation (for references see Ross *et al.*, 1997). For example, plants deficient in GA have dwarfed phenotypes and when external bioactive GA is given the normal phenotype is restored. The GA-metabolism (i.e. synthesis vs. inactivation of bioactive GA; Appendix 3) is, therefore, an important mechanism that controls thermoperiodic stem elongation. Results so far indicate that plants are reducing their level of GA₁ under negative DIF both by slowing down its biosynthesis and speeding up its inactivation (i.e. increased activity of the enzymes that convert GA₁ precursors into inactive forms of GA; Appendix 3). It becomes clear that negative DIF induced inhibition of internode elongation as a consequence of a reduced bioactive GA content in the plant tissue. Other hormones (e.g. auxins, cytokinins, abscisic acid and brassinosteroids) seem also to be involved in regulation of growth (see Chapter 2.4), but no information is available on their roles in DIF responses (Grindal *et al.*, 2000a).

In contrast to the effects of DIF on elongation, the effects of light quality on internode elongation operate via both influences on phytochrome status and changes in tissue sensitivity to GA. A close relationship between phytochrome, GA and extension growth has been demonstrated in several studies. In transgenic aspen (*Populus tremula* × *tremuloides*), the overexpression of phytochrome A (phyA) reduced internode length, and this was correlated with low levels of GA in the apical stem and leaf tissue (Olsen *et al.*, 1997). Similarly, transgenic tobacco and potato exhibited dwarfism with overexpressed phyA (Heyer *et al.*, 1995; Jordan *et al.*, 1995). PhyA deficient mutants of *Arabidopsis thaliana* were found to be relatively insensitive to FR suggesting that this phytochrome participates in the regulation of extension growth (Reed *et al.*, 1994).

Furthermore, the involvement of phytochrome (i.e. the light absorbing pigment that senses the relative amount of R and Fr light) in the DIF response is not clear, but its active form (Pfr; Appendix 5), which is obtained in the presence of R light, seems to be required for an effective negative DIF response. The different effectiveness of the DIF treatment observed among locations (see Chapter 2.1) is probably related to different irradiation levels and/or different photoperiods. When spinach (LD plant) is transferred from SD to LD conditions, this leads to an increase in GA₁, which is the primary active gibberellin for LD-induced stem elongation in spinach. Therefore, plants grown in longer photoperiods may produce high amounts of GA that may limit the negative DIF response.

3.3 Photoassimilates

Availability of carbohydrates is the basic principle for the growth of all the plant organs. Growth is dependent on the partitioning of assimilates to the elongation organs, and of the metabolism of the carbohydrates in these organs. Temperature is known to have only a minor effect on photosynthesis but that plays a strong role in the partitioning of assimilates among the different plant organs. However, the effects of DIF on photosynthesis are complex and not thoroughly studied. It is long since it was suggested that differential transport or availability of assimilates during day and night is causing the thermoperiodic effects on stem length (Went, 1957). However, there is still not enough data to support this suggestion (Grindal *et al.*, 2000a).

3.4 Water availability

Adequate water availability is needed to sustain elongation growth, especially because of cell elongation that is primarily based on water uptake. Kristoffersen (1963) studied thermoperiodicity in tomato and he hypothesised that lower temperatures during the night (positive DIF) increased cell growth and stem length as a consequence of a higher turgor pressure. Although there are no strong evidences to support such conclusion, Grindal *et al.* (2000a) expects that interactions between RH and DIF treatments are likely to be found for some species. For instance, high RH could possibly reduce the differences between DIF treatments. Since high EC combined with a drier crop strategy influences the water uptake of the roots (see Chapter 2.2) we also believe that these factors can interact with the DIF treatments.

3.5 General hypothesis for stem elongation process

Chrysanthemum (SD plant), capsicum and tomato (day neutral plants) and salvia (LD plant) show higher stem elongation rates (SER) during the night than during the day (Fig. 4; Bertram & Karlsen, 1995). In chrysanthemum and tomato it was found that SER is affected by the irradiance level, such that high irradiance during the day induces high SER during the following night (Bertram & Karlsen, 1994). This effect is clearly shown in Figure 4, especially when comparing the high values of SER during the scotoperiod of day 1 (a day with high irradiance during the photoperiod) with the lower values observed during the scotoperiod of day 2 (a day with low irradiance during the photoperiod). Furthermore, these authors also found that the main difference in SER between chrysanthemum plants grown under constant daily temperature and under a negative DIF occurred at night (Fig. 4). Although the described SER pattern seems to be the most common there were two exceptions reported in literature: petunia and euphorbia (Appendix 6). In petunia (LD plant) SER was largest during the day, whereas in euphorbia (SD plant) SER did not show large differences between photo- and scotoperiod (Bertram & Karlsen, 1994). The reasons for this differential SER pattern is not given by the authors, but since it is not related to the specific daylength response of flowering (e.g. chrysanthemum and euphorbia are both SD plants but have different SER patterns) we believe that this is possibly related to the sensitivity to DIF. DIF sensitive plants (Fig. 5) behave according to the general SER pattern described above.

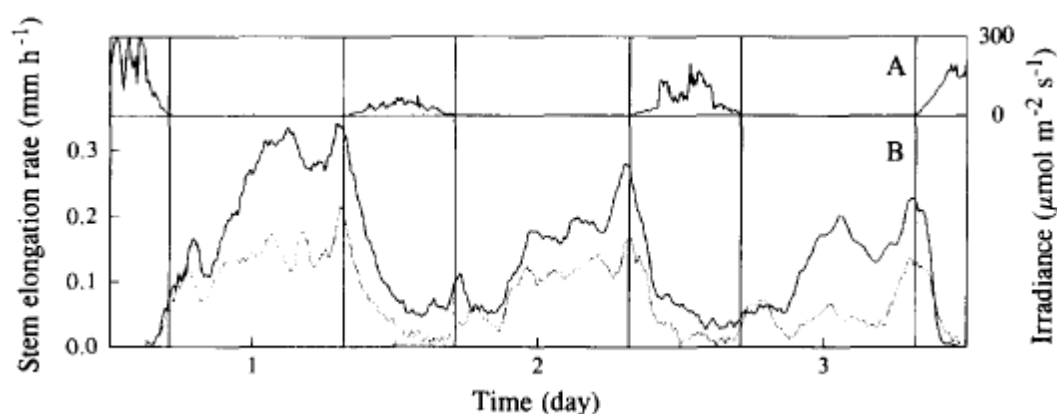


Figure 4. Stem elongation rate pattern of chrysanthemum over three days. The plants were grown at constant temperature (solid line) or DIF (dotted line). (A) Irradiance; (B) SER. Registration every 5 min (Source: Bertram & Karlsen, 1994).

For the general elongation pattern described above, we can formulate the following conclusion/hypothesis: the presence of sufficient levels of 'elongation requirements' (ERs), obtained during the preceding day, affect stem elongation during the night (Fig. 4). The nature of the ERs is unclear. As irradiance during the preceding day is important for elongation during the night, it might be that ERs are photosynthates. On the other hand, GA metabolism is involved in the stem elongation process and it has been suggested that temperature regime (DIF) affects elongation by influencing the GA synthesis and not by changing the sensitivity of the plant (Langton, 1998). Moreover, it seems that a light-on or a light-off signal triggers active GA production or interconversion (Fang *et al.*, 1991; Langton, 1998). This might suggest that parallel to the accumulation of photosynthates during the day, accumulation of inactive GAs takes place, which are converted to the active form by a light-off signal.

Thus, the first proposition for the internode elongation process of DIF-sensitive species is that accumulation of ERs is governed only by DT. The second proposition is that only NT governs the conversion of ERs into elongation. GA enhances the synthesis of enzymes such as invertase, which converts sucrose to glucose and fructose, thereby lowering the water potential which helps to maintain turgor (Miyamoto *et al.*, 1993, 2000). As stem elongation progresses, it will become increasingly hard to sustain turgor in the stem cells as their volume increases. It can be suggested that elongation may be limited by low turgor pressure insufficient to counter cell wall elasticity. The third

proposition for the internode elongation process is that it is limited by cell wall elasticity, which, as it is mainly a physical process, is governed both by DT and NT. The third proposition implies that, during the day, internode length decay may occur. Indeed, SER appeared to become negative for small periods during the day when chrysanthemum, salvia or capsicum were grown in a glasshouse, and these periods of apparent negative SER increased considerably when plants were grown under long-day compared to short-day treatments (Appendix 6, Fig. Chrysanthemum; Bertram & Karlsen, 1994). This indicates that stem elongation in glasshouses, started during the night, is sometimes turned into a stem length decay during the day; the longer the day, the stronger the effect. We expect this to happen due to a kind of negative feedback mechanism that is induced when a surplus of ER is accumulated during the day.

These hypotheses were successfully used for developing a process-based model for internode elongation in chrysanthemum (Schouten *et al.*, 2002). Furthermore, the three propositions explain the internode elongation process and its relationship with the growth conditions. For instance, in Chapter 2.1 on the 'Relevant interactions between climate conditions' it is stated that the effectiveness of the negative DIF is reduced at:

- i. Low light intensities – this can be explained by proposition 1 as the accumulation of ER takes place during the day. Taking into account that these ER are likely to be photoassimilates, it is easy to understand that low light intensities result in less photoassimilates and, therefore, elongation is itself limited (no additional effect of negative DIF);
- ii. Longer photoperiods (i.e. shorter night period) – this can be explained by proposition 1 and 2. Although under longer photoperiods photoassimilates are available, the duration of the night is the limiting factor as there are fewer hours to convert those assimilates into growth and, therefore, no additional effect of DIF is observed. Another explanation can be that under longer photoperiods more GA (also an elongation requirement) is produced counteracting the effect of the negative DIF.
- iii. Low R/Fr ratio – As mentioned above (Chapter 3.2) the presence of the active phytochrome seems to be needed for an effective negative DIF response. Another possibility is that the Fr effect on increasing concentration of bioactive GA is stronger than the effect of the negative DIF in decreasing GA concentration.

The role of the water availability in cell elongation is reflected in the third proposition. The effect of extreme short-days (ESD) in reducing stem length seems to be conflicting with the third proposition and with the findings that longer photoperiods reduce stem elongation. However, we believe that there are different reasons that lead to short plants both under very long photoperiods and under very short ones. As mentioned above very long photoperiods result in very short nights, where the limiting factor is not the accumulation of ER requirements but their conversion in elongation. In contrast, at ESD conditions the day period is very small and the accumulation of ER is not sufficient for the elongation resulting in shorter plants.

4 Practical applications (alternatives to chemical growth retardants)

Concern about the use of chemicals in horticultural crops has increased the attention on nonchemical methods of controlling plant growth (Bachman & McMahan, 2006). Several aboveground growth conditions have been described in Chapter 2 as being involved in the stem elongation process, including: temperature, light (intensity and quality), photoperiod, relative humidity, CO₂ concentration, plant density and pot size. Maintaining night temperature warmer than day temperature (negative DIF) and alteration of light quality have shown promise as nonchemical methods of controlling extension growth (Bachman & McMahan, 2006). Concerning the remaining aboveground growth conditions in spite of their significant effect on stem elongation (Chapter 2), it is important to keep in mind that these effects in practical terms are relatively small as compared to the effects of temperature and light quality. However when combining several growth conditions that limit stem elongation it is expected that a desired height control can be achieved.

From this study it can be concluded that in general stem elongation in floricultural crops is not principally a matter of assimilate availability. This conclusion is supported by extensive research in cut chrysanthemum where it was found that strongly enhancing the assimilate availability (with higher light intensity: from 4.2 to 18.3 mol m⁻²d⁻¹; higher CO₂ concentration: from 345 to 623 µmol mol⁻¹; or lower plant density: from 80 to 32 plants m⁻²) in spite of having a significant effect on plant height this was only increased with a maximum of 10% (Carvalho, 2003). Thus, a low assimilate availability can only be seen as a factor limiting stem elongation under very low natural irradiance levels or very high plant densities (Chapter 2). A practical application of these findings is that after a day of low irradiance it is not needed to apply a DIF treatment since the expected elongation during the following night is hampered by the lack of assimilates. Concerning the conditions in the root environment the manipulation of nutrients and water availability are the most promising strategies to reduce elongation.

4.1 DIF and DROP treatments

Besides the limitations pointed above (Chapter 2), the effect of DIF and DROP treatments on shoot length is not persistent after transfer to a common environment. In chrysanthemum it was found that, these treatments needed to be continued for most of the cultivation period to ensure that height reductions are visible at the marketing stage (Cockshull *et al.*, 1995). Nevertheless, according to Myster & Moe (1995) DIF and temperature DROP regimes can reduce or eliminate the use of growth retardants in many greenhouse crops. Four temperature strategies for plant height control have been implemented in commercial practice: constant day and night temperature, DIF, DROP, and a combination of DIF and DROP. The recommendations presented in Fig. 5 for some important greenhouse crops are based on experimental work that has been conducted in the last 20 years (Moe & Heins, 2000).

Temperature regime	Plant species
(1) Constant temperature	SDP: <i>Kalanchoe blossfeldiana</i>
(2) Negative DIF	SDP: Aster, Begonia, Chrysanthemum, Dahlia
NT	LDP: Antirrhinum, Campanula, Dianthus, Fuchsia, Petunia, Salvia
DT	DNP: Brassica, Citrullus, Cucumis, Cucurbita, Cyclamen, Gerbera, Impatiens, Lilium, Lycopersicum, Melissa, Ocimum, Pelargonium, Pisum, Viola
(3) DROP	SDP: Begonia, Euphorbia, Lilium, several bedding plants
NT	
DT	
(4) Negative DIF + DROP	In general: Same crops as reported for negative DIF and DROP. Very good effect on bedding plants (e.g. pansy)
NT	
DT	

Figure 5. Recommendation of different temperature regimes according to the species for limiting plant height in commercial greenhouse crops. Abbreviations: SDP = short day plants; LDP = long day plants; DNP = day neutral plants (Adapted from: Moe & Heins, 2000).

4.2 Manipulation of light quality

Changing the spectral distribution of the incoming light is an effective strategy for controlling stem elongation. This can be done in several ways: (i) manipulating plant density; (ii) using artificial light (e.g. light emitting diodes, LED); and (iii) using screening materials (e.g. photosensitive screens such as 'fluid roof system' and coloured plastic films; or blackout screens for excluding twilight) (for details see Chapter 2.1). Nevertheless, there are several reasons why these measures cannot be fully used in practice.

Concerning the manipulation of plant density, providing enough space to avoid elongation is not compatible with a cost efficient use of the greenhouse area (Grindal *et al.*, 2000b), and as referred above in most cases this would not be sufficient to reduce stem elongation to the desired levels. In practical terms, the possibility of using artificial lighting, with high levels of R and B light, for reducing elongation growth is only beneficial when natural light levels are low, otherwise the sunlight would dominate and dilute the effect of supplementary light (Grindal *et al.*, 2000b). As a general recommendation, the use of incandescent lamps (low R/Fr light) for day extension or night break treatments should be avoided when aiming at producing compact ornamental plants (Table 2; Moe *et al.*, 1991). High pressure sodium (HPS) lamps are more appropriate for that purpose (higher R/Fr ratio; Table 2). However, as mentioned above (Chapter 2.1) some plants react with increased elongation on supplementary light with HPS, but that is probably due to the lack of blue light compared to sunlight (Spaargaren, 2000). Light emitting diodes (LEDs) can be an interesting artificial light source when applying, for example, EOD light treatments as they offer the possibility of small and precise (narrow-band lighting: LEDs typically have about 10 nm band width) changes in intensity and spectral distribution (Lund *et al.*, 2007).

Concerning the use of photosensitive filters for stem elongation control of ornamental crops their effectiveness suggest a potential for commercial use (Chapter 2.1). However, since a low level of FR-light implies a high dye concentration, light transmission is strongly reduced, which has negative consequences for the total plant dry mass (Grindal *et al.*, 2000b), for plant quality (Clifford *et al.*, 2004) and for flower initiation or development of some long-day plants (Runkle & Heins, 2001). Consequently, these filters cannot be used during wintertime. According to Clifford *et*

et al. (2004) Fr-deficient environments have potential for height control of commercial poinsettia crops. However, light intensity must be optimised in order to avoid the problems mentioned above. These authors propose a dynamic management of the filters using automatic screening mechanisms. For example, the filters could be used only for a part of the cultivation period when elongation rate is higher (depending on the species) or only during specific moments of the day when the R/Fr ratio is naturally low (e.g. during twilight period; Chapter 2.1). Besides using photoselective films that filter Fr-light for eliminating the effect of the twilight period on internode elongation, the black-out screens commonly present in the greenhouses can be closed during that period. This was successfully done in easter lilies during the early spring in Canada (lat. 42°N) resulting in 10 to 25% shorter plants (Blom *et al.*, 1995; Blom & Kerec, 2003). However, a similar study was carried out in Norway (lat. 60°N) during summer using chrysanthemum and tomato plants but no or only a small effect was found on plant height (Mortensen & Moe, 1992a). The effects of twilight on elongation are not clear and might depend on the season and irradiance (Lund *et al.*, 2007). To better understand the effects of the EOD light quality on pot chrysanthemum Lund *et al.* (2007) created an artificial twilight using light-emitting diodes (LED). Their results were consistent with the ones from Canada, revealing the importance of eliminating the elongation effect of the twilight.

Another limitation to the use of Fr-deficient environment is mostly observed in LD plants (including pansy) where the light conditions that promote flowering also enhance stem extension (see Chapter 2.1). Therefore, commercial use of an Fr filter will be limited when a rapid and complete flowering of LDP is desired (Runkle & Heins, 2003). In general it can be concluded that additional studies are needed before implementing these light quality manipulation strategies.

4.3 Nutrients and water management

Regulation of nutrient supply offers an additional possibility to control plant height. Candidate nutrients that can be applied at suboptimal rates to regulate plant height are N, P and K, and possibly Ca and Mg. The application rates of these nutrients should not be too low, because this may lead to undesired effects on plant quality, such as leaf colour or brown spots. These so-called deficiency symptoms will especially occur, if nutrient supply is unbalanced. If the supply of all nutrients is decreased together to suboptimal levels, the risk for deficiency symptoms may be minimized. However, this reduced nutrient supply should not result in a better water availability (low EC) as this stimulates elongation. The supply of nutrients may be decreased directly by reduced fertilization or by indirect measures. Examples of indirect measures to decrease the P supply are the use of P buffers (e.g. Compalox) or clay. As mentioned above (Chapter 2.2) a certain degree of water stress is an important tool for producing compact ornamental plants. This is commonly done combining a higher EC and a drier cultivation strategy.

4.4 Plant breeding

Breeding for compact cultivars is an important tool for controlling plant height. According to Moe & Heins (2000) poinsettia already has new slow elongating cultivars. Shoots of such cultivars elongate slowly when plants are widely spaced but when the canopy closes the elongation of these shoots is strongly enhanced. This reveals that such cultivars are very sensitive to changes in light quality. A large genetic variation in terms of height is also present in kalanchoe (Carvalho *et al.*, 2005; 2008). Carvalho *et al.* (2005) studied twenty cultivars grown under the same conditions and found out that plant height varied between 10 and 32 cm and this variation was correlated with average vegetative internode length. It has been found that GA-deficient mutants of pea (Ross *et al.*, 1989) and tomato (Langton, 1998) show dwarfed phenotypes (Fig. 6). Similarly overexpression of phytochrome (e.g. phyA) reduced internode length in transgenic plants (for details see Chapter 3.2). An overview of the effects of the genome on GA metabolism is given by Ross *et al.* (2003). Rousseaux *et al.* (1997) investigated the possibilities of directing the overexpression of phyA to target organs (in our case this would be the internodes) using appropriate promoters, without eliminating the responsiveness in other parts of the plant. These authors successfully applied their strategy in tobacco plants. It is concluded that these biotechnological tools would constitute a valuable opportunity to control plant height.

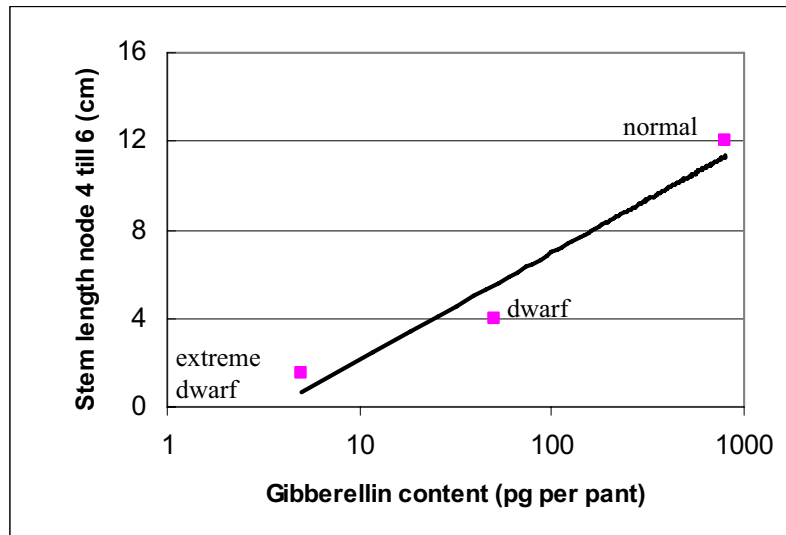


Figure 6. *Three pea genotypes with different GA content: the lower the GA content of a genotype, the more reduced stem elongation is (Ross et al., 1989).*

4.5 Conclusions

It is concluded that many factors have a significant effect on internode elongation. However, in most cases it will not be one single measure that will result in a compact plant. This study provides several possibilities that, in combination, can provide the desired height control. Part of these strategies are relatively easy to apply since they require little or no investment and only small interventions in the cropping systems are made. Table 3 gives an overview of the strategies discussed in this study as possible nonchemical alternatives for controlling plant height.

Table 3. Overview of the Strategies to Create Compact Floriculture Crops (partly based on E. Runkle, pers.comm.)

<p>I) Reduce number of internodes/ leaf number</p> <ul style="list-style-type: none"> • Provide the most inductive photoperiod so that flowering plants initiate flowers at an early physiological stage. With fewer vegetative nodes, plants will be more compact than plants under less inductive photoperiods • For plants that have a facultative irradiance response (flower at an earlier physiological age when provided with a high daily light integral), provide high light levels • Provide an 'optimal' cooling treatment to plants that have a facultative or obligate vernalization response. Crops with this response produce fewer nodes before flowering when exposed to a saturating cold treatment • Pinch plants (removal of shoot growth)
<p>II) Reduce internode elongation</p> <p>(a) Inhibit cell division</p> <ul style="list-style-type: none"> • Provide low ADT – plant development rates decrease with a decrease in the ADT. Lowering the growing temperature will slow down cell division, making plants shorter, but this does not have an effect on final plant height at maturity (the effect is transient)
<p>Inhibit cell expansion</p> <ul style="list-style-type: none"> • Provide a cool morning or day relative to the night (–DIF) • Provide a high R:Fr ratio by: <ul style="list-style-type: none"> ○ Using spectral filters that photoselectively reduce transmission of Fr light ○ Using blackout curtains so that plants are not exposed to twilight (which has a lower R:Fr) ○ Providing plants with supplemental/photoperiodic lighting that has a high R:FR (e.g. LED) ○ Growing plants at a wide spacing (low density) ○ Not hanging plants above a crop (foliage absorbs most R light but most of the FR is transmitted or reflected to crop below) • Apply plant growth retardants to inhibit gibberellin biosynthesis • Apply ethylene (ethephon) to plants (presumably interacts with GA biosynthesis?) • Use mechanical touching (brushing) or wind to increase ethylene biosynthesis • Provide supplemental (or an adequate amount of) blue light (this only seems effective on a minority of crops, mechanism is unknown but believed to be a cryptochrome response). Some species are taller when grown in an environment deficient in blue • Grow plants in small containers (presumably more drought stress) • Provide a limited amount of phosphorus, nitrogen and other elements • Limit water availability so that cell expansion is suppressed (limited osmotic potential so cell size is smaller)

5 Knowledge gaps and future research

Most of the effects of the aboveground as well as belowground growth conditions on stem elongation of several floricultural crops are well described in literature (Chapter 2). The few exceptions are related to the effectiveness of using LED or submitting the plants to ESD (Extreme Short Day) in order to reduce stem length. These strategies are described in literature but only a limited range of treatments in a limited number of plant species has been studied. Therefore, more detailed studies before applying these strategies are needed. From this report it also becomes clear that our understanding on how exactly the growth conditions influence stem elongation and how they interact with each other is very limited and represents a major gap in the knowledge. For instance, despite numerous studies on the effects of day and night temperature alternation on extension growth the physiological background which underlies the DIF/ DROP regimes are not fully understood, leading to uncertainties over how to optimise the use of temperature (Bertram & Karlsen, 1994; Langton, 1998). As shown in Chapter 3, strong evidences suggest the involvement of gibberellin (GA) metabolism in the regulation of stem extension, but further research is required before final conclusions can be drawn. Besides light (intensity, quality and photoperiod) other factors appear to interact with DIF to affect stem elongation, which makes these processes rather difficult to understand (Chapters 2 and 3). Several knowledge gaps have been identified and most of them are closely related to DIF. For instance, so far not much is known about: (i) the physiological basis of the interaction between DIF and phytochrome; (ii) GA metabolism concerning the way that negative DIF reduces the level of bioactive GA (Grindal *et al.*, 2000a). To fill in these gaps an extensive research on the topic would be required and perhaps that would not give straightforward answers to the grower practical questions. Some ideas for future research are listed below:

- Study the combined effects of DIF and phytochrome are of great interest since these factors are the most determinant for internode elongation and they interact with each other.
- Investigate the possibilities of light quality manipulation in the most sensitive periods for elongation. The phytochrome equilibrium (Pfr/Pr ratio) at the end of the day (EOD) and start of the dark period is very relevant for the elongation response. Therefore, using LED to provide a high R/FR ratio at the EOD or using black-out screens for elimination the twilight effect on stem elongation can be important measures. This would overcome the negative consequences of using filters and films continuously, which reduces total light levels too much in part of the season.
- Test the effectiveness of using ESD in a range of plant species, however, providing the same daily light integral to avoid a decrease in plant quality. Understand the principles behind the effect of ESD on elongation.
- Study the effectiveness of reducing plant height when combining several growth conditions (that individually are not enough for reducing plant height)
- Study the reasons behind the genetic variation in plant height (chapter 4) among different cultivars (e.g. Kalanchoe). The information obtained would be of utmost importance for enhancing breeding for shorter cultivars. Can dwarfing genes be induced, like in Geranium, Buttercup and pot gerbera. Switching off the shade avoidance response (phytochrome overexpressors and GA-mutants exist already in a number of species; Chapter 4.4).
- Optimisation of low nutrient strategies, e.g.:
 - Phase dependent phosphate treatment – ensure a low phosphate level around the stages of high stem elongation rate and supply enough phosphate during phases where phosphate is required e.g. initiation of shoots, bud and flower formation.
 - Development of a test that can measure how much phosphate will be available in the short term (within 1 to 2 weeks).
- Development of practical crop growth models based on growth curves and using knowledge about development and control of height, use of growth regulators and fine-tuning of the possibilities for irrigation and fertilization. Incorporation of this knowledge into practical crop control models based on light and temperature, (later) extended with irrigation, fertilization and crop growth retardants and/or growth regulators.

Literature

- Anonymus, 2001.
Plant hormones and growth regulators – effects on crop production. *Practical Hydroponics & Greenhouses* 1: 66-80.
- Anonymus, 2004.
Remproef in de belangstelling bij Dekker Chrysant. *Vakblad voor de Bloemisterij* 39: 48.
- Anonymus, 1988.
Met alar beheerst u de groei van uw planten. *Uitgave Ligtermoet chemie BV* 1-9.
- Armitage, A.M., 1994.
Growth regulation of bedding plant crops. *Ornamental bedding plants, chapter 3* p. 77-93
- Armitage, A.M. & T. Kowalski, 1983.
Effect of irrigation frequency during greenhouse production on the postproduction quality of *Petunia hybrida* Vilm. *J. Amer. Soc. Hort. Sci.* 108: 118-121.
- Armstrong, H., 2005.
Plants don't need so much phosphate. *Flowertech* 3 (8): 10-12.
- Baas, R., A. Brandts & N. Straver, 1995.
Growth regulation of bedding plants and poinsettia using low phosphorus fertilization and ebb and flow irrigation. *Acta Hortic.* 378: 129-137.
- Bachman, G.R. & M.J. McMahon, 1995.
Effects of spectral filters on growth of Easter lily. *Proc. Plant Growth Regulat. Soc. Amer.* 22: 344-347.
- Bachman, G.R. & M.J. McMahon, 2006.
Day and night temperature differential (DIF) or the absence of far-red light alters cell elongation in 'Celebrity White' in petunia. *J. Amer. Soc. Hort. Sci.* 131: 309-312.
- Barrett, J.E. & J.E. Erwin, 1994.
Bedding plant height control. *Bedding Plants IV*, chapter 16, 197-214. Ball Publishing.
- Beel, E., C. Piens & C. Dugardin, 1988.
De invloed van de aangehouden stikstofbemesting op de groei en bloei van *Azalea indica*. *Verbondsnieuws* 11: 551-553.
- Beer, C. de, 2000.
Geïntegreerde groeiregulatie bij Potchrysant. *PPO verslag* 2465.
- Benson, J.L., 1992.
Effects of spectral filters on bedding plant growth. MSc Thesis, Clemson University, South Carolina, USA.
- Berg, G. van den, 2003.
Groei remmen met koud water. *Vakblad voor de Bloemisterij* 47: 50-51.
- Bertram, L., 1992.
Stem elongation of Dendranthema and tomato plants in relation to day and night temperatures. *Acta Hortic.* 327: 61-69.
- Bertram, L. & P. Karlsen, 1994.
Patterns in stem elongation rate in chrysanthemum and tomato plants in relation to irradiance and day/night temperature. *Sci. Hortic.* 58: 139-150.
- Bertram, L. & P. Karlsen, 1995.
Kinetics and circadian rhythms of stem elongation in greenhouse plants. *Acta Horti.* 378: 53-60.
- Biesheuvel, C. & M. Hermesen, 1988.
Remmen van potplanten - Precieze methode moeilijk aan te geven. *Vakblad voor de Bloemisterij* 6: 42-43.
- Blacquiere, T.J., 1997.
Planthormonen en groeiregulatoren, *ongepubliceerd overzicht*. PBN, 1997.
- Blom, T.J. & D.R. Kerec, 2003.
Effects of far-red light/temperature DIF and far-red light/temperature pulse combinations on height of lily hybrids. *J. Hort. Sci. Biotech.* 78: 278-282.

- Blom, T.J., M.J. Tsujita & G.L. Roberts, 1995.
Far-red end of day and reduced irradiance affect plant height of easter and Asiatic hybrid lilies. *HortSci.* 30: 1009-1012.
- Blom, T. & D. Kerec, 2004.
Irrigation Method and Temperature of Water Affect Height of Potted Easter Lilies. *HortSci.* 39: 11-203.
- Borch, K., 1997.
Roots, P supply and ethylene. *Abstract of Workshop 'The influence of cultivation conditons on the keeping quality of ornamentals in Denmark.*
- Bragg, N.C. & A.K. Fuller, 1997.
Cultural control of plant growth – a fresh look. *Acta Hortic.* 450: 535-544.
- Brum, B., V.J. Santos, M.A. Rodrigues, R.A. Bellé & S.J. Lopes, 2007.
Growth, duration of the growing stages and inflorescences production of chrysanthemum under different prunings and size of pot. *Ciência Rural* 37: 682-689.
- Carvalho, S.M.P., 2003.
Effects of growth conditions on external quality of cut chrysanthemum: analysis and simulation. Ph.D. dissertation, Wageningen University, The Netherlands, 171pp.
- Carvalho, S.M.P. & E. Heuvelink, 2001.
Influence of greenhouse climate and plant density on external quality of chrysanthemum (*Dendranthema grandiflorum* (Ramat.) Kitamura): First steps towards a quality model. *J.Hort. Sci. & Biotech.* 76: 249-258.
- Carvalho, S.M.P., E. Heuvelink, R. Cascais & O. Van Kooten, 2002.
Effect of day and night temperature on internode and stem length in chrysanthemum. *Ann. Bot.* 90: 111-118.
- Carvalho, S.M.P., E. Heuvelink & B.A. Eveleens, 2005.
Plant height formation in different cultivars of kalanchoe. *Acta Hortic.* 691: 83 - 90.
- Carvalho, S.M.P., S.E. Wuillai & E. Heuvelink, 2006.
Combined effects of light and temperature on product quality of *Kalanchoe blossfeldiana*. *Acta Hortic.* 711: 121 - 126.
- Carvalho, S.M.P., J. Almeida, B.A. Eveleens, M.J. Bakker & E. Heuvelink, 2008.
Modelling visual quality of *Kalanchoe blossfeldiana*: influence of cultivar and pot size. *Acta Hortic.* (in press).
- Cathey, H.M., 1974.
Participation of phytochrome in regulating internode elongation of *Chrysanthemum morifolium* (Ramat) Hemsl. *J. Amer. Soc. Hortic. Sci.* 99: 17-23.
- Sun, Y.W., J.J. Chen, M.J. Tseng, W.N. Chang & T.F. Sheen, 2000.
The role of growth regulators on cold water for irrigation reduces stem elongation of plug-grown tomato seedlings. *Chinese Journal of Agrometeorology* 7: 61-68.
- Cipollini, D.F., 1999.
Cost to flowering of the production of a mechanically hardened phenotype in *brassica napus*. *Int. J. Plant. Sci.* 160: 735-741.
- Clifford, S.C., E.S. Runkle, F.A. Langton, A. Mead, S.A. Foster, S. Pearson & R.D. Heins, 2004.
Height control of poinsettia using photoselective filters. *HortSci.* 39: 383-387.
- Cockshull, K.E., F.A. Langton & C.R.J. Cave, 1995.
Differential effects of different DIF treatments on Chrysanthemum and Poinsettia. *Acta Hortic.* 378: 15-25.
- Cuijpers, L.H.M. & J.V.M. Vogelezang, 1992.
DIF and temperature drop for short-day pot plants. *Acta Hortic.* 327: 25-32.
- Dalal, S.R., V.S. Gonge, A.G. Pimple, Rajeshwari Deshmukh & Swarupa Utgikar, 2005.
Response of phosphorus levels to growth, flowering, yield and flower quality of gerbera under polyhouse. *Annals of Plant Physiology* 19: 120-121.
- Davis, T.D. & A.S. Andersen, 1989.
Growth retardants as aids in adapting new floricultural crops to pot culture. *Acta Hortic.* 252: 77-85.
- Dijkstra, T., 2004.
Fosfaatbuffer remt groei eenjarige zomerbloeiers. *Vakblad voor de Bloemisterij* 14: 57.
- Dijkstra, T., 2007.
Hortensia remmen met gebruik van hulpstoffen. *Gewasnieuws Hortensia*, jaargang 9, nummer 2, p3.

- Duckett, C.M. & C.W. Lloyd, 1994.
Gibberellic acid-induced microtubule reorientation in dwarf peas is accompanied by rapid modification of an alpha-tubulin isotype. *Plant J.* 5: 363-372.
- Duijn, B van, 2003.
Groeiremming met niet-chemische methode (eerste fase). *Gepubliceerd door TNO/DLV.*
- Eng, R.Y.N., M.J. Tsujita & B. Grodzinski, 1985.
The effects of supplementary HPS lighting and carbon dioxide enrichment on the vegetative growth, nutritional status and flowering characteristics of *Chrysanthemum morifolium* Ramat. *J. Hortic. Sci.* 60: 389-395.
- Erwin, J.E., 1991.
Thermomorphogenesis in plants. Ph.D. Dissertation, Michigan State University, East Lansing, 165 pp.
- Erwin, J.E. & R.D. Heins, 1995.
Thermomorphogenic responses in stem and leaf development. *Hortsci.* 30: 940-949.
- Erwin, J.E., R.D. Heins & M.G. Karlsson, 1989.
Thermomorphogenesis in *Lilium longiflorum*. *Amer. J. Bot.* 76: 47-52.
- Erwin, J.E., P. Velguth & R.D. Heins, 1994.
Day/night temperature environment affects cell elongation but not division in *Lilium longiflorum* Thunb. *J. Exp. Bot.* 45: 1019-1025.
- Erwin, J.E., M. Ascemo, F. Pfeger & R.D. Heins, 1992a.
New Guinea *Impatiens* production. *Minn. Comm. Flow. Grow. Bull.* 41: 1-15.
- Eveleens, B.A., E. Heuvelink & F.R. Van Noort, 2007.
Invloed van EC en RV op de groei en kwaliteit van Kalanchoë. Bleiswijk : Wageningen UR Glastuinbouw, 34 pp.
- Fang, N., B.A. Bonner & L. Rappaport, 1991.
Phytochrome mediation of gibberellin metabolism and epicotyl elongation in cowpea, *Vigna sinensis* L. In: Takahashi N, Phinney BO, MacMillan J, eds. *Gibberellins*. New-York: Springer Verlag, 280-288.
- Garner, L. & F.A. Langton, 1997.
Brushing pansy transplants: a flexible, effective method for controlling plant size. *Sci. Hort.* 70: 187-195.
- Garner, L., F.A. Langton & T. Björkman, 1997.
Commercial adaptations of mechanical stimulation for the control of transplant growth. *Acta Hortic.* 435: 219-230.
- Gessnitzer, H., 1997.
Vermeidbare Fehler bei der Primelkultur. Erfahrungen eines praktikers. *Deutscher Gartenbau* 7: 420-422.
- Gislerød, H.R. & P.V. Nelson, 1997.
Effect of relative air humidity and irradiance on growth of *Dendranthema × grandiflorum* (Ramat.) Kitamura. *Gartenbauwissenschaft* 62: 214-218.
- Graaf-van der Zande, M.T.H., 1986.
Hoge EC nog geen groeiregulator bij perkplantenteelt. *Vakblad voor de Bloemisterij* 47: 31-33.
- Grindal, G., 1997.
Thermoperiodic stem elongation in Pisum sativum L. and Cucumis sativus L. – the role of gibberellins and phytochrome. Ph.D. thesis 1997: 27. Agricultural University of Norway.
- Grindal, G., O. Junttila & A. Ernstsén, 2000a.
Physiological basis of thermoperiodic responses in plants. In: Strømme E., ed. *Advances in floriculture research*. Report no. 6/2000. Agricultural University of Norway. Oslo: Spekter, 65-74.
- Grindal, G., L.M. Mortensen & R. Moe, 2000b.
Manipulation of the daylight spectre for growth control. In: Strømme E., ed. *Advances in floriculture research*. Report no. 6/2000. Agricultural University of Norway. Oslo: Spekter, 75-82.
- Grantzau, E., 2006.
Ein knapper Rohstoff. *Der Gartenbau* 2: 16-18.
- Gugenhan, E., 1999.
Kompakte pflanzen durch zartes streicheln. *DeGa* 46: 27-28.
- Hansen, C.W. & K.L. Nielsen, 2001.
Reduced phosphorus availability as a method to reduce chemical growth regulation and to improve plant quality. *Plant Nutrition*, vol. 92.p.314-315. *Kluwer Academic Publishers*.

- Hansen, C.W., 2005.
Growth regulation of ornamentals in Europe – focus on alternative methods. Proceedings – plant growth regulation society of america – annual meeting – vol 32, p.53-56.
- Hansen, C.W., 1997.
Root activity – growth and photosynthesis in relation to P supply. *Abstract of Workshop 'The influence of cultivation conditons on the keeping quality of ornamentals in Denmark'*.
- Hansen, C.W. & J. Lynch, 1998.
Response to phosphorus availability during vegetative and reproductive growth of chrysanthemum I en II. *J Amer. Soc. Hort. Sci.* 123: 215-229.
- Hansen, C.W., K.K. Petersen & A.K. Larsen.
Effects of reduced nutrient and water availability on plant growth and post-production quality of Hibiscus rosa-sinensis. *Acta Hortic.* 669: 269-273.
- Hansen, C.W. & K.K. Petersen.
Reduced nutrient and water availability to Hibiscus rosa-sinensis "Cairo Red" as a method to regulate growth and improve post-production quality. *Europ. J. Hortic. Sci.* 69: 159-166.
- Hansen, H.T., L. Hendriks, E. Ueber & A.S. Andersen, 1996.
Effect of a low temperature period (Drop) during different periods on morphogenesis of Dendranthema 'Surf', Fuchsia 'Beacon', Verbena 'Karminrosa', and Pelargonium 'Pulsar Red'. *Gartenbauwissenschaft* 61: 188-196.
- Healy, W. & S. Klick, 1993.
Potting method improves flowering of alstroemeria. *Acta Hortic.* 337: 19-24.
- Heemers, L., 2000.
Geïntegreerde groeiregulatoren in de potplantenteelt: een haalbaar alternatief. *Verbondsnieuws* 11: 28-31.
- Heij, G. & P.J.A.L. De Lint, 1987.
CO₂ and night temperature on growth and development of chrysanthemum. *Acta Hortic.* 197: 125-131.
- Heins, R.D. & H.F. Wilkins, 1979.
The influence of node number, light source, and time of irradiation during darkness on lateral branching and cutting production in 'Bright Golden Anne' chrysanthemum. *J. Amer. Soc. Hortic. Sci.* 104: 265-270.
- Heins, R.D. & J.E. Erwin, 1990.
Understanding and applying DIF. *Greenhouse Grower* 8: 73-78.
- Hendriks, L. & E. Ueber, 1995.
Alternative methods of regulating the elongation growth of ornamental plants: a current assessment. *Acta Hortic.* 378: 159-167.
- Hendriks, L., M. Fischer & H. Schilling, 2000.
Steuern statt stauchen – wasserstress bei Pelargonien hat viele wirkungen. *Gärtnerbörse* 17: 14-15.
- Henny, R.J., 1986.
Increasing basal shoot production in a non branching Dieffenbachia hybrid with BA. *HortSci.* 21: 1386-1388.
- Henny, R.J., 1991a.
A review of literature concerning the use of growth retardants on tropical foliage plants. *Foliage Digest*, vol. 14, march: 4-8.
- Henny, R.J., 1991b.
A review of literature concerning the use of growth regulators to induce lateral or basal shoot production in ornamental tropical foliage plants. *Foliage Digest* vol 14, june: 3-6.
- Hermann, P., 1967.
Further possibilities for the use of Cycocel for pot plants. *Gartenwelt* 67: 263-264.
- Heuvelink, E., 1989.
Influence of day and night temperature on the growth of young tomato plants. *Sci. Hortic.* 38: 11-22.
- Heuvelink, E., U. Van Meeteren, L.N. Chang, G. Fancello & J.H. Lee, 1998.
The influence of temperature, photoperiod and plant density on external quality of cut chrysanthemum. *XXV International Horticultural Congress*, Brussels, August 1998, Book of Abstracts, 314.
- Heyer, A.G., D. Mozley, V. Landschütze, B. Thomas & C. Gatz, 1995.
Function of phytochrome A in potato plants as revealed through the study of transgenic plants. *Plant. Physiol.* 109: 53-61.

- Hughes, A.P. & K.E. Cockshull, 1972.
Further effects of light intensity, carbon dioxide concentration, and day temperature on the growth of *Chrysanthemum morifolium* cv. Bright Golden Anne in controlled environments. *Annals Bot.* 36: 533-350.
- Huld, A. & N.E. Andersson, 1997.
The influence of plant density and gradual shading on vegetative growth of *Dendranthema*. *Acta Hort.* 435: 209-217.
- Jacobsen, L. & M.G. Amsen, 1992.
The effect of temperature and light quality on stem elongation of chrysanthemum. *Acta Hort.* 305: 45-50.
- Jagers op Akkerhuis, F. & C. Wang Hanssen, 2002.
Fosfaatbuffer biedt alternatief voor chemische groeiremmers. *Vakblad voor de Bloemisterij* 17: 56-57.
- Janssen, E. & R. Verkade, 1997.
Groeibeheersing. *Vakblad voor de Bloemisterij* 8: 59.
- Jensen, E., S. Eilertsen, A. Ensten, O. Juntilla & R. Moe, 1996.
Thermoperiodic control of stem elongation and endogenous gibberellins. *J. Plant Growth Reg.* 15: 167-171.
- John, A.Q., S.S. Saini & P.P. Sharma, 1984.
Effect of nitrogen, phosphorus and plant spacing on growth and flowering of pansy. *South Indian Hortic.*
- Jordan, E.T., P.M. Hatfield, D. Hondred, M. Talon, J.A.D. Zeevaart & R.D. Vierstra, 1995.
Phytochrome A overexpression in transgenic tobacco. *Plant Physiol.* 107: 797-805.
- Khattak, A.M. & S. Pearson, 1997.
The effects of light quality and temperature on the growth and development of chrysanthemum cvs Bright Golden Anne and Snowdon. *Acta Hort.* 435: 113-121.
- Kristoffersen, T., 1963.
Interactions of photoperiod and temperature in growth and development of young tomato plants (*Lycopersicon esculentum* Mill). *Physiol. Plant. Suppl. t.* 1-97.
- Krijger, D., 2002.
Alternatieve groeiremming kuipplanten. *PPO* 2002.
- Krijger, D., 2004.
Alternatieve remmethoden kuipplanten. *PPO* 2004
- Kromwijk, A., 2001a.
Groeiremming bij primula acaulis – voorstudie naar alternatieve remmethoden en toegestane chemische middelen. *PPO* 2001.
- Kromwijk, A., 2001b.
Planmatige teeltstrategie Poinsettia, *PPO*, project 41-2426.
- Kromwijk, A., 2002.
Toetsing planmatige teeltstrategie poinsettia. *PPO* 2002.
- Kruijf, de, 1993.
Groeiregulatoren. *Vakblad voor de Bloemisterij* 30: 38-39.
- Langton, F.A., 1998.
Regulation of stem extension by temperature. In: Cockshull KE, Gray D, Seymour GB, Thomas B, eds. *Genetic and environmental manipulation of horticultural crops*. New York: CABI Publishing, 191-203.
- Langton, F.A. & K.E. Cockshull, 1997a.
A re-appraisal of DIF extension growth responses. *Acta Hort.* 435: 57-64.
- Langton, F.A. & K.E. Cockshull, 1997b.
Is stem extension determined by DIF or by absolute day and night temperatures? *Sci. Hort.* 69: 229-237.
- Leeuwen, G.J.L. van, 1992.
Groeiregulatie bij Pelargonium door middel van EC. *Proeftuin Noord Nederland, verslag 30*.
- Leeuwen, G.J.L. van, 1994.
Groeiregulatie door middel van fosfaatbeperking(1). *Verslag Proeftuin Noord Nederland*.
- Leeuwen, G.J.L. van, 1995.
Groeiregulatie door middel van fosfaatbeperking(2). *Verslag Proeftuin Noord Nederland*.
- Leth, P. van, 2005.
Tilt vooral van belang als groeiremmer. *Vakblad voor de Bloemisterij* 29: 40-41.

- Lewis, D., M. Prasad, N. Borst & M. Spiers, 1994.
Effect of N-P-K fertiliser on the growth of *Limonium perigrinum* 'Ballerina Rose'. *New Zealand Journal of Crop and Horticultural Science* 22: 217-220.
- Liptay, A., P. Sikkema & W. Fonteno, 1998.
Transplant growth control through water deficit stress – a review. *Hortech.* 8: 540-543.
- Logt, B. van der, 1997.
Groeiregulatie Pelargonium, *Stageverslag PBN* 1997.
- Looman, B., 1994.
Tilt 250EC, een nieuw effectief middel voor bestrijding roest. *Vakblad voor de Bloemisterij* 50: 31.
- Lörcks, H., J. Klatt & A. Sommer, 2004.
Pflanzenschäden durch fungizide und wachstumsregulatoren. *Zierpflanzenbau* 24: 30-31.
- Ludolph, D., 1990.
Licht an Hibiscus. *Deutscher Gartenbau* 19: 1266.
- Ludolph, D., 1992.
Height control of ornamental plants without chemical growth retardants. *Ohio Flor. Bull.* 748: 14.
- Lukassen, I. & C. Vermeulen, 2006.
Onderzoek naar de invloed van hulpstoffen op de effectiviteit van de remstof chloormequat (CeCeCe) in de teelt van Poinsettia. *DLV-Facet*, Wageningen 2006.
- Lindstrøm RS. 1968. Supplemental carbon dioxide and growth of *Chrysanthemum morifolium* Ram. *Proc. Amer. Soc. Hortic. Sci.* 92: 627-632.
- Lund, J.B., T.J. Blom & J.M. Aaslyng, 2007.
End-of-day lighting with different Red/Far-red ratios using light emitting diodes affects plant growth of *Chrysanthemum × morifolium* Ramat. 'Coral Charm'. *HortSci.* 42: 1609-1611.
- Maas, F.M. & J. van Hattum, 1998.
Thermomorphogenic and photomorphogenic control of stem elongation in *Fuchsia* is not mediated by changes in responsiveness to gibberellin. *J. Plant Growth Regul.* 17: 39-45.
- Marschner, H., 1995.
Mineral nutrition of higher plants. *Academic Press*, London, 889 pp.
- McMahon, M.J. & J.W. Kelly, 1990.
Control of poinsettia growth and pigmentation by manipulating light quality. *HortSci.* 25: 1068 (Abstr.).
- McMahon, M.J. & J.W. Kelly, 1999.
CuSO₄ filters influence flowering of chrysanthemum cv. Spears. *Sci. Hortic.* 79: 207-215.
- McMahon, M.J., J.W. Kelly & D.R. Decoteau, 1991.
Growth of *Dendranthema grandiflorum* (Ramat.) Kitamura under various spectral filters. *J. Amer. Soc. Hortic. Sci.* 116: 950-954.
- McMahon, M.J. & J.W. Kelly, 1990.
Influence of spectral filters on height, leaf chlorophyll, and flowering of *Rosa × hybrida* 'Meirutral'. *J. Environ. Hort.* 8: 209-211.
- Meulen, R. van der & B. van Duijn, 2004.
Trillen kan mogelijk chemisch remmen vervangen. *Vakblad voor de Bloemisterij*, 1:48-49.
- Miyamoto, K., J. Ueda & S. Kamisaka, 1993.
Gibberellin-enhanced sugar accumulation in growing subhooks of etiolated *Pisum sativum* seedlings: Effects of gibberellic acid, indoleacetic acid and cycloheximide on invertase activity, sugar accumulation and growth. *Physiol. Plantarum* 88: 301-306.
- Miyamoto, K., E. Ito, H. Yamamoto, J. Ueda & S. Kamisaka, 2000.
Gibberellin-enhanced growth and sugar accumulation in growing subhooks of etiolated *Pisum sativum* seedlings: Effects of actinomycin D on invertase activity, soluble sugars and stem elongation. *J. Plant Physiol.* 156: 449-453.
- Moe, R., 1990.
Effect of day and night temperature alternations and of plant growth regulators on stem elongation and flowering of the long-day plant *Campanula isophylla* Moretti. *Sci. Hortic.* 43: 291-305.
- Moe, R. & R.D. Heins, 1990.
Control of plant morphogenesis and flowering by light quality and temperature. *Acta Hort.* 272:81-90.

- Moe, R. & R.D. Heins, 2000.
Thermo- and photomorphogenesis in plants. In: Strømme E., ed. *Advances in floriculture research*. Report no. 6/2000. Agricultural University of Norway. Oslo: Spekter, 52-64.
- Moe, R., R.D. Heins & J. Erwin, 1991.
Stem elongation and flowering of the long-day plant *Campanula isophylla* Moretti in response to day and night temperature alternations and light quality. *Sci. Hortic.* 48: 141-151.
- Moe, R. & L.M. Mortensen, 1992.
Thermomorphogenesis in pot plants. *Acta Hortic.* 305: 19-25.
- Mortensen, L.M., 1986a.
Effect of intermittent as compared to continuous CO₂ enrichment on growth and flowering of *Chrysanthemum × morifolium* Ramat. and *Saintpaulia ionantha* H. Wendl. *Sci. Hortic.* 29: 283-289.
- Mortensen, L.M., 1986b.
Effect of relative humidity on growth and flowering of some greenhouse plants. *Sci. Hortic.* 29: 301-307.
- Mortensen, L.M., 2000.
Effects of air humidity on growth, flowering, keeping quality and water relations of four short-day greenhouse species. *Sci. Hortic.* 86: 299-310.
- Mortensen, L.M. & R. Moe, 1983.
Growth responses of some greenhouse plants to environment. VI. Effect of CO₂ and artificial light on growth and flowering of *Chrysanthemum × morifolium* Ramat. *Sci. Hortic.* 19: 141-147.
- Mortensen, L.M. & R. Moe, 1992a.
Effects of selective screening of the daylight spectrum and of twilight on plant growth in greenhouse. *Acta Hort.* 305: 103-108.
- Mortensen, L.M. & R. Moe, 1992b.
Effects of various day and night temperature treatments on morphogenesis and growth of some greenhouse and bedding plant species. *Acta Hort.* 327: 145-153.
- Mortensen, L.M. & E. Strømme, 1987.
Effects of light quality on some greenhouse crops. *Sci. Hortic.* 33: 27-36.
- Mulderij, B., 1998.
Eénjarige zomerbloeiërs: EC en kwaliteit. *PBG* 1998.
- Murakami, K., H. Cui, M. Kiyota, I. Aiga & T. Yamanae, 1997.
Control of plant growth by covering materials for greenhouses which alter the spectral distribution of transmitted light. *Acta Hortic.* 435: 123-130.
- Myster, J. & R. Moe, 1995.
Effect of diurnal temperature alternations on plant morphology in some greenhouse crops: a mini review. *Sci. Hortic.* 62: 205-215.
- Neumaier, D. & R. Röber, 2003.
Compalox im test. *DEGA* 32: 36-37.
- Nielsen, K.L., C.W. Hansen & C.O. Ottosen, 1998.
Effect of P availability and elevated CO₂ growth, whole-plant gas exchange, and stress tolerance of potted miniature roses. Abstract from *Workshop Wageningen* 'Improving post harvest behaviour of ornamentals.
- Olsen, J.E., O. Juntilla, J. Nilsen, M.E. Eriksson, I. Martinussen, O. Olsson, G. Sandberg & T. Moritz, 1997.
Ectopic expression of oat phytochrome A in hybrid aspen changes critical daylength for growth and prevents cold acclimatization. *Plant J.* 12: 1339-1350.
- Oosterkamp, H., 2000.
Effect van klei in potgrond – plateau- klei uit zweden. Bara mineral AB, Malmövägen, Sweden. 24 pages.
- Oyaert, E., E. Volckaert & P.C. Debergh, 1999.
Growth of chrysanthemum under coloured plastic films with different light qualities and quantities. *Sci. Hortic.* 79: 195-205.
- Parups, E.V., 1978.
Chrysanthemum growth at cool night temperature. *J. Amer. Soc. Hortic. Sci.* 103: 839-842.
- Pearson, S., P. Hadley & A.E. Wheldon, 1995.
A model of the effect of day and night temperatures on the height of chrysanthemums. *Acta Hortic.* 378: 71-79.

- Pitchay, D.S., 2002.
Impact of 11 elemental nutrient deficiencies on shoot and root growth, and foliar analysis standards of 13 ornamental taxa with emphasis on Ca and B control of root apical meristem development. *PhD-thesis, North Carolina State University*, 321 pp.
- Potter, I. & S.C. Fry, 1993.
Xyloglucan endotransglycosylase activity in pea internodes: Effects of applied gibberellic acid. *Plant Physiol.* 103: 235-241.
- Quispel, A. & D. Stegwee, 1983.
Plantenfysiologie. *Bont, Scheltema & Holkema*, Utrecht/Antwerpen.
- Rajapakse, N.C. & J.W. Kelly, 1992.
Regulation of chrysanthemum growth by spectral filters. *J. Amer. Soc. Hortic. Sci.* 117: 481-485.
- Rajapakse, N.C. & J.W. Kelly, 1995.
Spectral filters and growing season influence growth and carbohydrate status of chrysanthemum. *J. Amer. Soc. Hortic. Sci.* 120: 78-83.
- Rajapakse, N.C., M.J. McMahon & J.W. Kelly, 1993.
End of day far-red light reserves height reduction of chrysanthemum induced by CuSO₄ spectral filters. *Sci. Hortic.* 53: 249-259.
- Rajapakse, N.C., R.E. Young, M.J. McMahon & R. Oi, 1999.
Plant height control by photoselective filters: current status and future prospects. *HortTechnol.* 9: 618-624.
- Reed, J.W., A. Nagatani, T.D. Elich, M. Fagan & J. Chory, 1994.
Phytochrome A and phytochrome B have overlapping but distinct functions in *Arabidopsis* development. *Plant Physiol.* 104: 1139-1149.
- Richter, M., 2004a.
Niedrigere Hortensien met reduzierter fosfatdüngung. *Zierpflanzenbau jahrgang 104*: seite 5, 22.
- Richter, M., 2004b.
Hortensien: weniger hemmstoffe mit geringer P-düngung, *Zierpflanzenbau jahrgang 104*: seite 24, 26.
- Röber, R. & W. Horn, 1993.
Wirkung unterschiedlicher wassergaben auf wachstum, qualität und prolingealt von Euphorbia pulcherrima willd.ex Klotzsch. *Gartenbauwissenschaft* 58: 15-20.
- Rooij, E. de & H. Verberkt, 2005.
Remmiddelen in opkweek hortensia beïnvloeden trekresultaten sterk. *Vakblad voor de Bloemisterij* 38: 52-53.
- Ross, J.J., J.B. Reid & S.M. Swain, 1993.
Control of stem elongation by gibberellin A1: evidence from genetic studies including the slender mutant *sin*. *Aust. J. Plant Physiol.* 20: 585-599.
- Ross, J.J., J.B. Reid, P. Gaskin & J. MacMillan, 1989.
Internode length in *Pisum*: estimation of GA₁ levels in genotypes Le, le and le^d. *Physiol Plant* 76: 173-176.
- Ross, J.J., I.C. Murfet & J.B. Reid, 1997.
Gibberellin mutants. *Physiol. Plant.* 100: 550-560.
- Rousseaux, M.C., C.L. Ballaré, E.T. Jordan & Vierstra, 1997.
Directed overexpression of *PHYA* locally suppresses stem elongation and leaf senescence responses to far-red radiation. *Plant, Cell & Environ.* 20: 1551-1558.
- Ruamrugsri, S., T. Ohyama, T. Konno & T. Ikarashi, 1996.
Deficiency of N, P, K, Ca, Mg or Fe mineral nutrients in Narcissus cv. 'Garden Giant'. *Soil Science and Plant Nutrition* 42: 809-820.
- Runkle, E.S. & R.D. Heins, 2001.
Specific functions of red, far red, and blue light in flowering and stem extension of long-day plants. *J. Amer. Soc. Hortic. Sci.* 126: 275-282.
- Runkle, E.S. & R.D. Heins, 2003.
Photocontrol of flowering and extension growth in long-day plant Pansy. *J. Amer. Soc. Hortic. Sci.* 128: 479-485.
- Sach, L., 1995.
The effect of difference in temperature regimes (DIF) on pot chrysanthemum and bedding plants. *Acta Hortic.* 378: 81-86.

- Schouten, R.E., S.M.P. Carvalho, E. Heuvelink & O. Van Kooten, 2002.
Modelling of temperature-controlled internode elongation applied to chrysanthemum. *Ann. Bot.* 90: 353-359.
- Schröder, Richter M., 2004.
P-buffer Compalox als hemmstof bei hortensien? *Zierpflanzenbau* 5: 20-21.
- Schussler, H.K. & A. Kosiba, 2006.
Effect of extreme short day treatment (ESD) on the development and appearance of *Calibrachoa* hybr. Cerv. and *Scaevola saligna* G. Forst. *Acta Hort.* 711: 297-300.
- Serek, M. & A.S. Andersen, 1994.
Polyamine uptake does not affect floral longevity in miniature potted roses. *HortSci.* 29: 196-198.
- Spaargaren, J.J., 2000.
Belichting van tuinbouwgewassen. Uitgave Hortilux Schröder B.V. Monster. 178 pp.
- Straver, N., 1994.
P-beperking in de bemesting bij *Euphorbia pulcherrima*, *PBN Aalsmeer*, 1994
- Straver, N., 1996.
Fosfaatbemestingproeven bij *Begonia*, *Dieffenbachia*, *Ficus* en *Saintpaulia*, PBG Aalsmeer.
- Straver, N., 1999.
Bemestingadviesbasis potplanten. *PBG Aalsmeer*, 1999.
- Stavang, J.A., J. Olsen & R. Moe, 2006.
The role of light and gibberellin deactivation in thermoperiodic stem elongation - a mini review. *Acta Hort.* 711: 381-384.
- Starman, T.W., J.W. Kelly & H.B. Pemberton, 1989.
Characterization of ancymidol effects on growth and pigments of *Helianthus annuus* cultivars. *J. Amer. Soc. Hort. Sci.* 114:427-430.
- Strøm, M. & R. Moe, 1997.
DIF affects internode and cell extension growth and cell number in *Campanula isophylla* shoots. *Acta Hort.* 435: 17-24.
- Taiz, L. & E. Zeiger, 2002.
Plant Physiology (third edition). Sinauer Associates 2002. 661 p.
- Tangerås, H., 1979.
Modifying effects of ancymidol and gibberellins on temperature induced elongation in *Fuchsia × hybrida*. *Acta Hort.* 91: 411-417.
- Ueber, E., 2001.
Kontrollierte Düngung – ein hemmstoffersatz. *Taspo* 8:34-37.
- Ueber, E., 2002.
Maseman S. Gezielter P-mangel kann hemmstoffe nicht ersetzen. *Dega* 14:39-41 *PBN proefverslag* 1508-30.
- Veerman, A., 1988.
Goed spuiten belangrijk voor effect – alar in de sierteelt. *Vakblad voor de Bloemisterij* 16: 59.
- Vegter, B. & H. Verberkt, 2007.
Belichting van potplanten vooral voor betere kwaliteit. *Vakblad voor de Bloemisterij* 6: 50-52.
- Verberkt, H., 1992.
Invloed substraat, watergeeffrequentie en bemesting op *Impatiens New Guinea*.
- Verberkt, H., 1993.
Invloed EC op groei *Impatiens New Guinea*. *PBN, Proefverslag* 1508-31.
- Verberkt, H., M.A. de Jong, A. Bulle & D. van der Bree, 1996.
EC heeft duidelijke invloed op groei en bloei Potchrysant. *Vakblad voor de Bloemisterij* 23:44-45.
- Verberkt, H., 1995.
Belichtingstrategieën bij potplanten 1. rapport 11. PBG Aalsmeer.
- Verberkt, H., M.A. de Jong & R. Schaefer, 1996.
Invloed voedingsconcentratie (EC) op groei en kwaliteit Kalanchoë. *PBG, rapport* 61.
- Verberkt, H., R. Schaefer & B. van der Logt, 1998.
Groeiregulatie *Pelargonium*. *PBG rapport* 125.
- Verberkt, H., 1999.
Remregels potchrysant 1999, *PBG intern verslag*.

- Verberkt, H., C. de Beer & M. de Jongh, 2001.
Implementatie van een teeltstrategie voor planmatige productie van Kalanchoë met minimale inzet van groeiregulatoren. *PPO intern rapport*.
- Vogelezang, J., R. Moe, H. Schüssler, L. Hendricks, L. Cuijpers & E. Ueber, 1992.
Cooperative European research on temperature strategies for bedding plants. *Acta Hort.* 327: 11-16.
- Vos, Roose de, 1988.
Groeiregulatoren: auxines zijn meer dan bewortelingshormonen. *Verbondsnieuws* 13:660-663.
- Warmenhoven, M., 2003.
Alternatieve groeibeheersing Primula. *PPO-rapport 575*, 24 pp.
- Warmenhoven, M. & F.R. van Noort, 2005.
Fosfaatbeperking in éénjarige zomerbloeiërs, *PPO* 2005.
- Warmenhoven, M. & F.R. van Noort, 2007.
Vervolg fosfaatonderzoek, nog niet gepubliceerd 2007.
- Went, F.W., 1944.
Plant growth under controlled conditions. II. Thermoperiodicity in growth and fruiting of the tomato. *Amer. J. Bot.* 31: 135-150.
- Went, F.W., 1957.
The experimental control of plant growth. *Chron. Bot.* 17.
- Wever, G., R. Postma, E.J.W. Wattel-Koekkoek, C. de Kreij, A. Bulle, A.M.M. van der Burg & J.B.G.M. Verhagen, 2004.
Sturing kwaliteit en houdbaarheid potplant door toevoeging van klei aan substraten. *PPO-rapport*, 76 pp. 2004.
- Yoneda, K., M. Usui & S. Kubota, 1997.
Effect of nutrient deficiency on growth and flowering of Phalaenopsis. *Journal of the Japanese Society for Horticultural Science* 66: 141-147.
- Zeevaart, J.A.D., D.A. Gage & M. Talon, 1993.
Gibberellin- A_1 is required for stem elongation in spinach. *Proc. Nat. Acad. Sci. USA*. 90: 7401-7405.
- Zieslin, N. & M.J. Tsujita, 1988.
Regulation of stem elongation of lilies by temperature and the effect of gibberellin. *Sci. Hortic.* 37: 165-169.

Appendix I.

Effect of DIF and DROP treatments on stem elongation of several plant species (In: Myster & Moe, 1995)

	Strong or medium effect		Little or no effect	
	DIF	DROP	DIF	DROP
Flowering short day plants				
<i>Aster novi-belgii</i> L.			52	
<i>Begonia</i> × <i>hiemalis</i> Fortsch.	1, 3, 4, 5	2, 3, 6		3, 5
<i>Chrysanthemum</i> L. sp.	4, 7, 8, 9, 10, 11			4, 10
<i>Dahlia</i> Cav.	47			
<i>Euphorbia pulcherrima</i> Willd. ex Klotzsch	2, 4, 12, 13, 42, 43	2, 4, 12, 43		
<i>Kalanchoe blossfeldiana</i> v. Poelln.			2, 4	2
Flowering long day plants				
<i>Antirrhinum majus</i> L. as cut flower	59			
<i>Antirrhinum majus</i> L. as bedding plant			58	
<i>Campanula isophylla</i> Moretti	2, 14, 15, 16, 44			44
<i>Dianthus</i> L. sp.	17, 18			
<i>Fuchsia</i> × <i>hybrida</i> Hort. ex Vilm.	19, 20, 21, 22, 45, 50			45
Flowering day neutral plants				
<i>Cyclamen persicum</i> Mill.	41			
<i>Gerbera jamesonii</i> H. Bolus ex Hook. f.	51		29	
<i>Impatiens walleriana</i> Hook. f.	22, 55			23
<i>Lilium longiflorum</i> Thunb.	19, 23, 24, 49	23, 49		
<i>Passiflora caerulea</i> L.			32	
<i>Pelargonium</i> L'Hér. ex Ait. sp. seed	53, 56			5, 31
<i>Pelargonium</i> L'Hér. ex Ait. sp. cuttings			5, 22, 30	
<i>Petunia</i> × <i>hybrida</i> Hort Vilm. - Andr.	5, 25, 46		5	5
<i>Rosa</i> L.			26, 27	26, 27
<i>Salvia splendens</i> F. Sellow ex Roem. & Schult	5			5, 23
<i>Viola wittrockiana</i> Gams.	28			
Many foliage plants			33	
Plant propagation of vegetables as				
<i>Brassia</i> L.	34, 35			34
<i>Citrullus</i> Schrad	54			
<i>Cucumis</i> L.	36, 37, 54, 57	38		
<i>Cucurbita</i> L.	48			
<i>Lycopersicon</i> Mill.	37, 39, 48, 54	38, 40		10
<i>Phaseolus</i> L.			54	
<i>Pisum</i> L.			48, 54	
<i>Zea</i> L.	48, 54			
Pot herbs				
<i>Melissa officinalis</i> L.	28			28
<i>Ocimum basilicum</i> L.	28			28

1, Willumsen and Moe, unpublished data, 1994; 2, Moe and Mortensen, 1992a; 3, J. Myster and R. Moe, unpublished data, 1995; 4, Cuijpers and Vogelegang, 1992; 5, Mortensen and Moe, 1992a; 6, Grindal and Moe, 1994; 7, Jacobsen and Amsen, 1992; 8, Karlsson et al., 1989; 9, Hendriks, 1991; 10, Bertram, 1992; 11, Mortensen and Moe, 1987; 12, Moe et al., 1992a; 13, Berghage and Heins, 1988; 14, Moe and Heide, 1985; 15, Moe, 1990; 16, Moe et al., 1991; 17, Moe, 1983; 18, Moe, 1991; 19, Erwin et al., 1989b; 20, Erwin et al., 1991c; 21, Tangerås, 1979; 22, Vogelegang et al., 1992; 23, Erwin, 1991; 24, Erwin and Heins, 1990a; 25, Kaczperski et al., 1988; 26, Moe and Mortensen, 1992b; 27, Mortensen and Moe, 1992b; 28, Ronglan and Vågen, 1991; 29, Næss, 1991; 30, Jensen, 1992c; 31, Erwin et al., 1992b; 32, Jensen, 1992a; 33, Jensen and Andersen, 1992; 34, A.K. Bakken, unpublished data, 1994; 35, Berge, 1991; 36, Grimstad and Frimanslund, 1993; 37, De Koning, 1992; 38, Grimstad, 1993; 39, De Koning, 1992; 40, Gertson, 1992a; 41, Hendriks and Scharpf, 1987; 42, Langton et al., 1992; 43, Ueber and Hendriks, 1992; 44, Ihlebekk, 1993; 45, Hendriks, 1991; 46, Stupa, 1993; 47, Brøndum and Heins, 1993; 48, Erwin and Heins, 1990b; 49, Erwin and Heins, 1991; 50, Erwin and Kovanda, 1990; 51, Erwin et al., 1991b; 52, Anderson, 1992; 53, Halvorsen, 1993; 54, Erwin et al., 1993; 55, Erwin and Heins, 1993; 56, Erwin and Schwarze, 1993; 57, Agrawal et al., 1993; 58, Erwin and Heins, 1994; 59, J.E. Erwin and J. Myster, unpublished data, 1995.

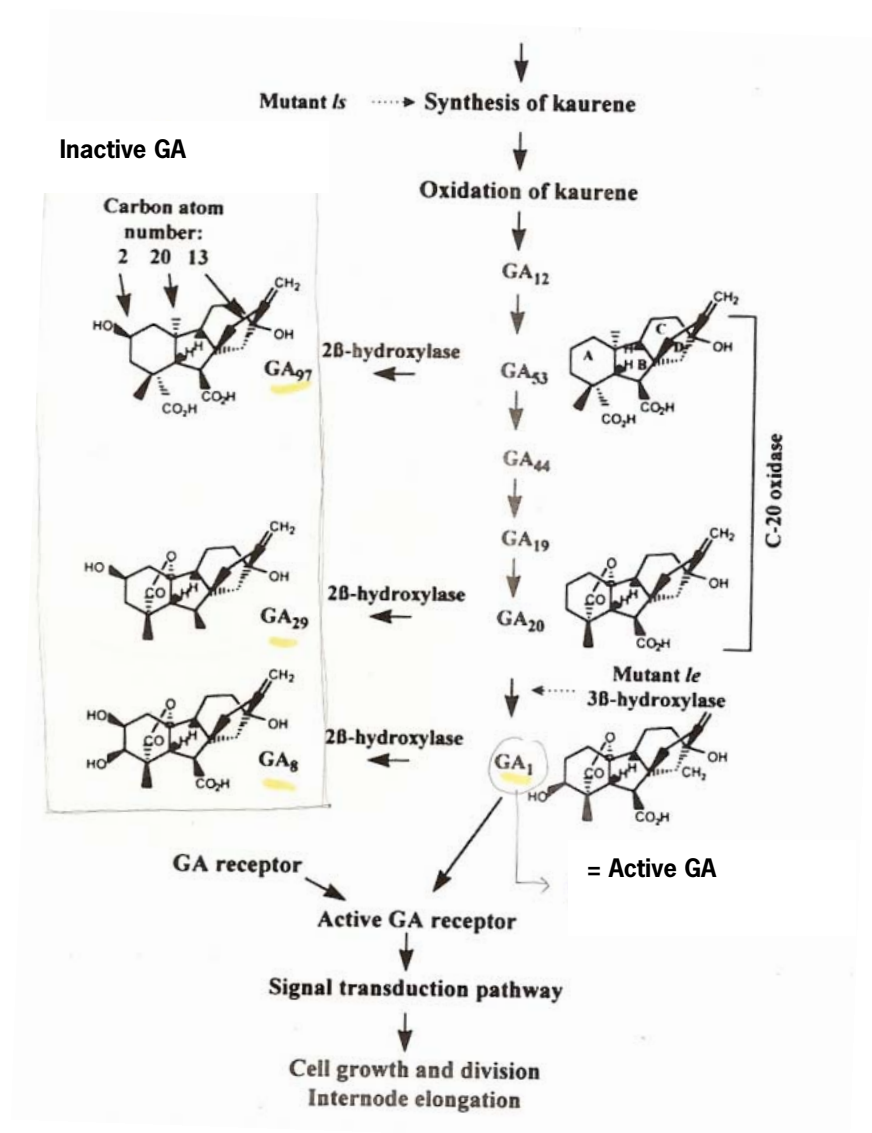
Appendix II.

Essential plant nutrients: their relative amounts in plants, functions and classification

Name	Chemical symbol	Relative % in plant*	Function in plant	Visual deficiency symptoms
Nitrogen	N	100	Proteins, amino acids	Light green to yellow appearance of leaves, especially older leaves; stunted growth
Phosphorus	P	6	Nucleic acids, ATP	Leaves may develop purple coloration; stunted plant growth and delay in plant development
Potassium	K	25	Catalyst, ion transport	Older leaves turn yellow initially around margins and die
Calcium	Ca	12.5	Cell wall component	Reduced growth or death of growing tips
Magnesium	Mg	8	Part of chlorophyll	Initial yellowing of older leaves between leaf veins spreading to younger leaves
Sulphur	S	3	Amino acids	Initial yellowing of young leaves spreading to whole plant; similar symptoms to nitrogen deficiency but occurs on new growth
Iron	Fe	0.2	Chlorophyll synthesis	Initial distinct yellow or white areas between veins of young leaves leading to spots of dead leaf tissue
Copper	Cu	0.01	Component of enzymes	
Manganese	Mn	0.1	Activates enzymes	Interveinal yellowing or mottling of young leaves
Zinc	Zn	0.03	Activates enzymes	Interveinal yellowing on young leaves; reduced leaf size
Boron	B	0.2	Cell wall component	Death of growing points and deformation of leaves with areas of discoloration
Molybdenum	Mo	0.0001	Involved in N fixation	
Chlorine	Cl	0.3	Photosynthesis reactions	

Appendix III.

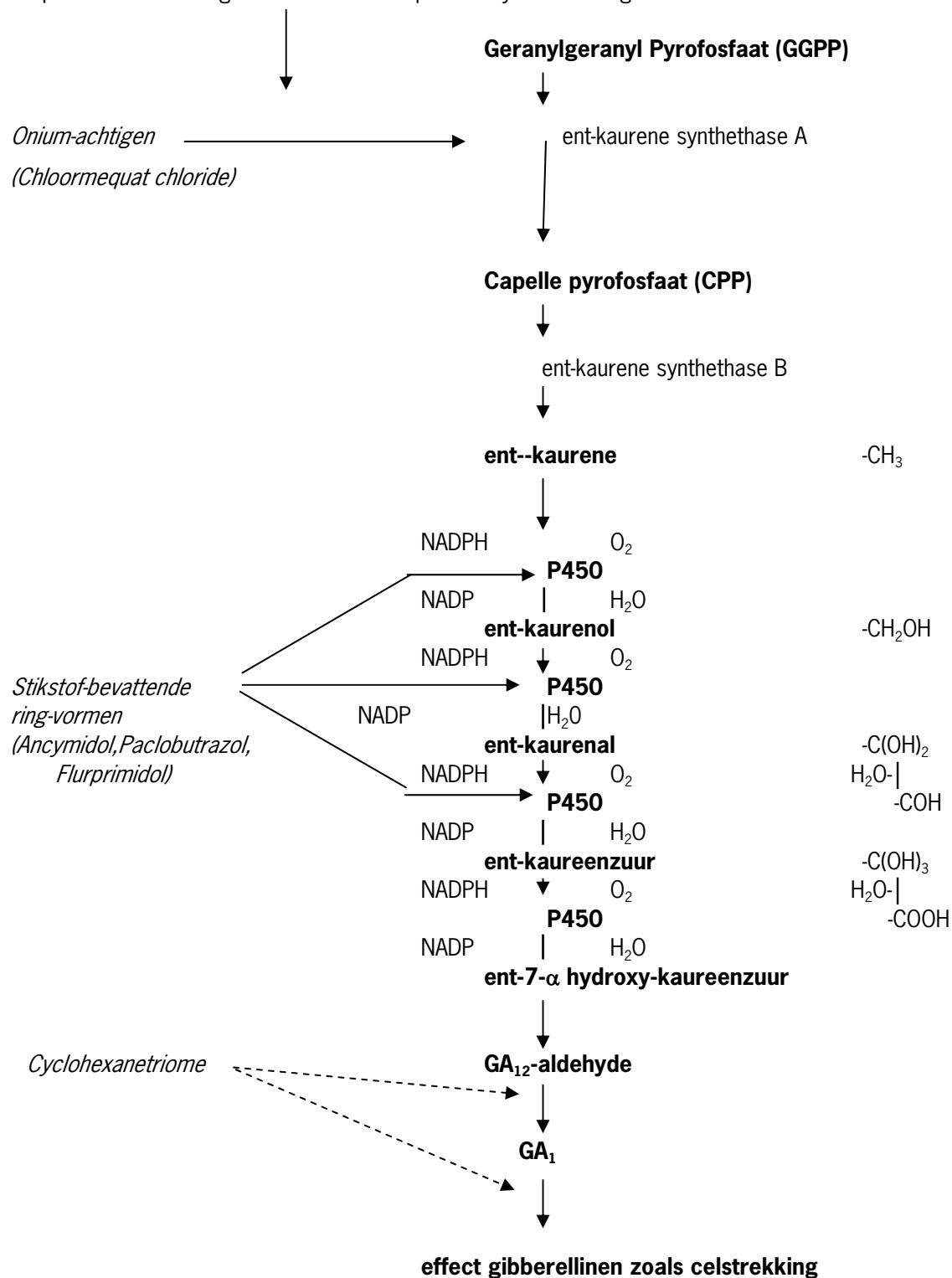
GA₁ metabolism in plants (e.g. pea). A similar pathway is leading to GA₄ but in that case GA₁₂ is not hydroxylated at carbon 13. (In: Grindal *et al.*, 2000a)



Appendix IV.

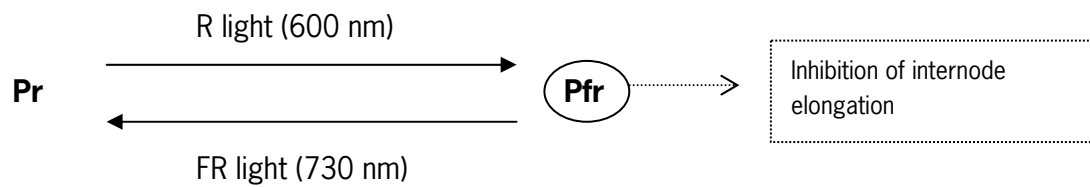
Effect of growth retardants on the biosynthesis of gibberellins

De plaats van inwerking van remmiddelen op de biosynthese van gibberellinen



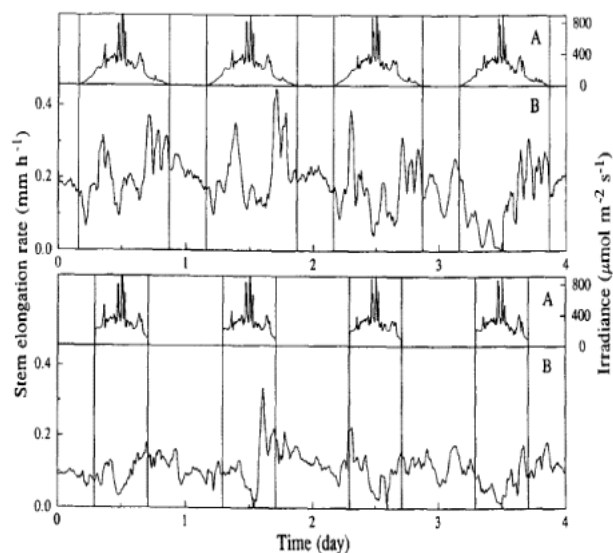
Appendix V.

Red (R) and far-red (FR) light initiate inter-conversion of the two forms of phytochrome. For instance, a relative high amount of R light over FR light establishes a pool of Pfr that results in inhibition of internode elongation

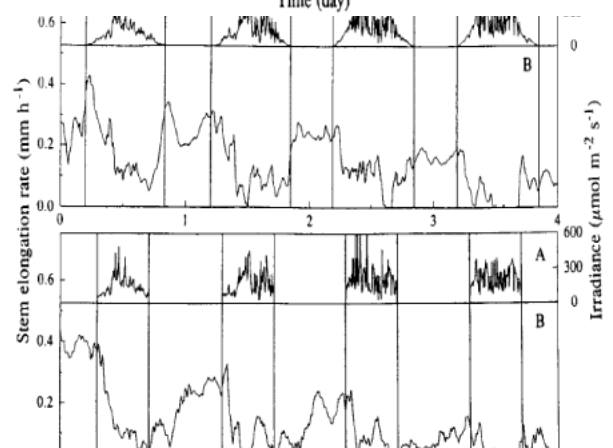


Appendix VI.

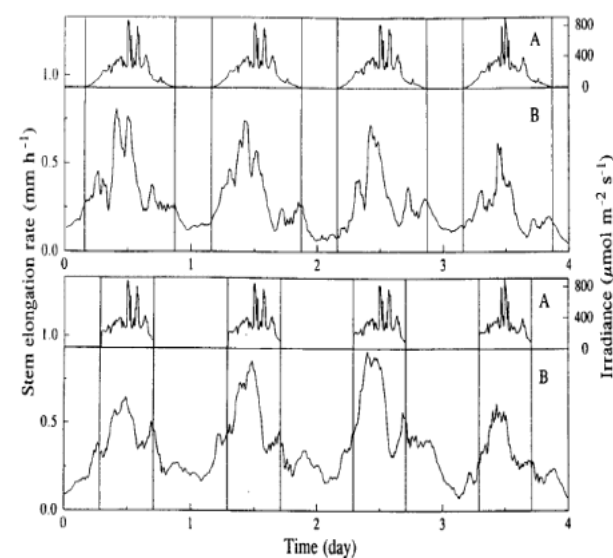
Stem elongation rate (SER) of chrysanthemum, euphorbia and petunia grown under long-day (upper figure within each specie) or short-day (lower figure within each specie) conditions. A: irradiance; B: SER. In: Bertram & Karlsen (1995)



Chrysanthem



Euphorbia



Petuni

Appendix VII.

Possibilities for compact plants (DLV Facet, 2005)

Tabel. Geïntegreerde groeiregulatie mogelijkheden eenjarige zomerbloeiers

Methoden	met risico		zonder risico	
	effect		Opmerkingen	
Gewas- en raskeuze			Compacte en uniforme rassen kiezen. Praktisch moeilijk ivm assortiments-versmalling. Via veredeling veelal langdurig traject en kan ten koste gaan van andere goede eigenschappen. Daarbij moeten eenjarige zomerbloeiers zich wel weer krachtig ontwikkelen zodra ze in de tuin bij de consument staan.	
Negatieve DIF en kouval			Hier zijn bij diverse gewassen goede resultaten te behalen. De scheutuitloop kan echter achterblijven en bloeiverlating (en kleinere bloemen) kunnen optreden als de gewenste etmaaltemperatuur niet gehaald wordt. Neg DIF en Kouval zijn echter niet het gehele seizoen toepasbaar ivm. oplopende dagtemperaturen in het voorjaar. Toepassing geldt voor een hele kasafdeling en kan niet per partij uitgevoerd worden.	
Licht en globale straling			Wordt al zoveel mogelijk toegepast bij de teelt van eenjarige zomerbloeiers. Er wordt vrijwel niet geschermd.	
Lage fosfaatgift en/of compalox			Effect sterk gewasafhankelijk. Stuurbaarheid moet verder worden ontwikkeld. De toepassing is voor telers nog te beperkt en niet zonder gevaren.	
Trillen en aaien			Werkt bij een aantal gewassen goed. Mogelijkheden naar inpasbaarheid op de bedrijven is in ontwikkeling. Vindt o.a. plaats bij de opkweek van komkommerplanten.	
Droog telen			Moeilijk uniform realiseerbaar, kan daarnaast kwaliteitsverlies geven.	
Hoge EC (= fysiologisch droog telen)			Moeilijk uniform realiseerbaar, kan daarnaast kwaliteitsverlies geven.	
Kleurenspectrum groeilicht / stuurlicht	?	?	Is nog in een experimenteel stadium. Niet in onderzoek bij eenjarige zomerbloeiers.	
Remmiddelen			Goed werkzaam om de groei subtiel te regelen. Gebruik staat onder druk i.v.m. milieu en kosten. Met name bij snel groeiende gewassen zal gezocht moeten worden naar versterking van de remmende werking van de middelen door toevoegingen van hulpstoffen, andere combinaties, toedieningstechnieken of nieuwe remmiddelen om de efficiëntie per eenheid w.s. te verhogen.	

