

Thermo- and Photomorphogenesis in Plants

Introduction

Temperature and light are two very important factors for growth and development of greenhouse crop. Light drives photosynthesis and influences plant growth and morphology. Temperature is the primary environmental factor affecting rate of plant development. In addition it influences plant morphogenesis. Light and temperature also interact with other growth factors such as carbon dioxide, air humidity, water supply and nutrition. Much research has been directed toward the development of proper temperature and lighting strategies for efficient greenhouse production. In the early 1940s, Dr. F. W. Went and co-workers investigated the optimum day and night temperature combinations for plant growth in the first air-conditioned greenhouse, a phytotron at the California Institute of Technology. They found that tomato plants grew taller under a combination of a high temperature during the light period and a lower temperature during the dark period than when grown under constant temperature. The ability of the plants to discriminate between temperature during the day and night in their response to flowering, fruiting and growth, was referred to as thermo-periodism (Went, 1944). Went concluded that the sugar transport to growing tissue was restricted under high night temperatures (NT), which resulted in restricted growth. Kristoffersen (1963) continued the work on tomato in Went's laboratory in the early 1950s and subsequently in Norway. He found that daily temperature alternations strongly enhanced stem elongation under high day temperature (DT) and low NT combinations. He argued that low NT improved the water balance in the plant and this was the main reason for enhanced stem elongation. He introduced the phytotron technology to Norway; this technology had a great impact on the research on controlled climates the following 30 years in Norway. The initial research work of Went and Kristoffersen did not focus on using temperature as tool for height control.



Fig. 1. The effect of 25 day (DT) and night temperature (NT) combinations on plant height of *Campanula isophylla* 'Blue' grown in a daylit phytotron in summer under natural long days (18-19 hrs) at the Agricultural University of Norway. DT, from left to right: 12, 15, 18, 21 and 24 °C, NT from upper to lower row of plants: 12, 15, 18, 21 and 24 °C.

The energy crises in the mid 1970's lead to a new series of experiments on the influence of DT and NT alternations on plant growth. Low NT resulted in a considerable energy saving in greenhouses with single glass and no thermal screens compared to warmer NT. However, initial experiments in 1976 in a phytotron with 25 combinations of DT and NT on *Campanula isophylla* showed that a combination of low NT and high DT enhanced stem elongation, while the opposite temperature regimes, low DT and high NT, resulted in dwarf, compact plants (Fig. 1).

Similar reactions were found in *Fuchsia x hybrida*, *Dendranthema grandiflorum* and *Euphorbia pulcherrima* (Tangerås 1979). The *Campanula* experiment was demonstrated during an ISHS symposium in 1976 at the Agricultural University of Norway where Professor Harold Wilkins from University of Minnesota, USA observed the results. Wilkins showed the results to his PhD student, Royal Heins, and when he started his career at Michigan State University in 1978, he continued experiments with diurnal temperature alternations on some important floriculture crops. He and his co-workers introduced the term **thermomorphogenesis** (Erwin et al. 1989). They defined thermoperiodic effects on plant morphology as thermoperiodic responses. They also introduced the DIF-concept which describes the relationship between DT and NT, a concept that has become a very useful tool for application of temperature as a tool for height control in commercial greenhouse production. The results from the early DT/NT alternation experiments in the 1970s led some growers to produce crops with the DT almost equal to NT. However, using a higher NT than DT was not economical until the use of thermal screens and double acrylic sheets or plastic greenhouse covers became more common in the 1980s. Application of growth retardants to control plant height and quality was a common practice, and many different chemical growth retardants were available. Tightened regulations focusing on the environment, and increasing costs for governmental registration of chemicals have influenced the availability of growth retardants. For example in Norway, only chlormequat (Cycocel), daminozide (Alar), flurprimidol (Topflor) and paclobutrazol (Bonzi) has the necessary registration for application in ornamental plants at present. No growth retardants are legal for use on seedlings or plants of edible crops. The only exception is chlormequat application for height control in cereals. This situation has resulted in an increased interest in breeding dwarf cultivars, as well as finding alternatives to chemical height control.

The DIF-concept

Erwin et al. (1989) showed that the effects of diurnal temperature alternation on stem length in *Lilium longiflorum* could be best described by the mathematical difference (DIF) between DT and NT (DT minus NT) in the 10 to 26 °C range, rather than by independent responses to DT and NT. Internode length of *Lilium* increased as DIF increased from -16 to +16 °C. Similar relationships between DIF and stem elongation have been reported for a wide range of plant species (Myster and Moe 1995, Erwin and Heins 1995). Typical DIF response curves relating plant height at anthesis and DIF is shown for the long-day plant *Campanula isophylla* and internode length in *Lilium longiflorum* (Fig. 2). Leaf number was little affected by DIF and therefore, *Campanula* plants grown under negative DIF have short internodes, similar to that shown for *Lilium* (Fig. 2).

Some other important morphogenetic responses to negative DIF include:

- (1). Reduced length of internodes, petioles, flower stems and flower peduncles, and of leaf size. Anatomical studies showed that differences in internode elongation and leaf expansion were a result of differences in cell elongation in *Lilium* and both cell elongation and cell division in *Campanula*. Under negative DIF, both processes were inhibited and this may be a result of reduced gibberellin activity in the sub-apical meristem (see Grindal et al., page 68). Leaf and shoot orientation become more horizontal compared with a more upright orientation when positive DIF is applied.
- (3). Leaf chlorophyll content may decrease under negative DIF, resulting in plants appearing chlorotic. Seedlings seem to be more sensitive than adult plants. A

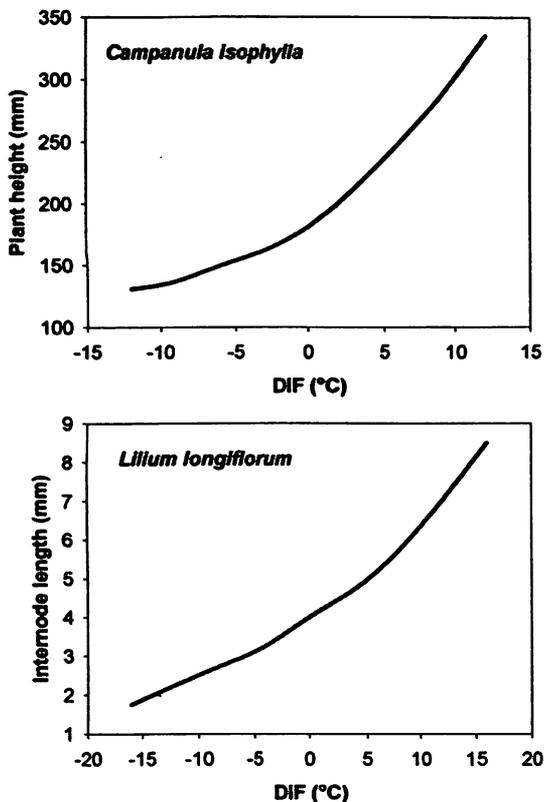


Fig. 2. Response curve describing the relationship between the difference (DIF) between day temperature (DT) and night temperature (NT) and plant height at anthesis of the long day plant *Campanula isophylla* 'Alba' and internode length of plants of *Lilium longiflorum* 'Nellie White'. Circles and squares represent mean plant height or internode length for each treatment. Number of internodes was not significantly affected by treatments. (from Erwin et al. 1989 and Moe 1990).

change from negative to positive DIF greens up the leaves within a few day/night cycles. (4). The magnitude of response to DIF is not the same across all values of DIF; internode elongation decreases more from positive to zero DIF than from zero to negative DIF in some species. In other species the relationship between elongation and DIF is linear, and in some cases only poor relationships are reported if the plants have a different optimum DT and NT for elongation and flowering (Grindal, 1997). The DIF concept seems to be most valid as long as DIF treatments are compared with the same average daily temperature (ADT). (5). DIF has the greatest effect on stem elongation during the stage of rapid growth. Therefore, negative DIF treatment at an early stage of stem elongation is important for proper height control, (6). ADT has only a small influence on internode length and plant height, but increasing ADT enhances leaf unfolding and

flower development rate. In some SDP, a high NT delays flower initiation and can modify the ADT or DIF effects on rate of development.

The description and subsequent introduction of the DIF concept to greenhouse growers has resulted in the successful application of negative DIF for height control on a wide range of pot plants, bedding plants, and seedlings. The greatest success is reported in poinsettia and Easter lilies. Application of negative DIF has reduced the application of growth regulators to a minimum, and made the crop more environmental friendly and economically sound. The negative DIF application is still restricted to a few crops in practice due to limited information of how negative DIF affects plant shape in hundred of different species grown for sale. Some species are not sensitive to negative DIF at all and other tools for height control are required.

Temperature drop concept

Plant stem elongation is also sensitive to a short period (about two hours) temperature drop (referred later to as Drop, sometimes called temperature DIP in the

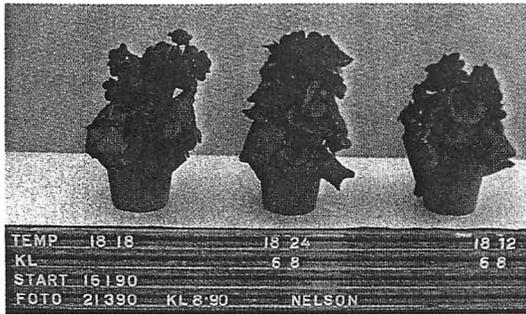


Fig. 3. The effect of a 2-hour Drop from 18 to 12°C (to the right) during the last two hours of the night or a temperature increase from 18 to 24°C (in the middle) on plant height in *Begonia x hiemalis* 'Nelson'. The control plant (to the left) was grown at constant 18°C. The drop treatment had no significant effect on flowering.

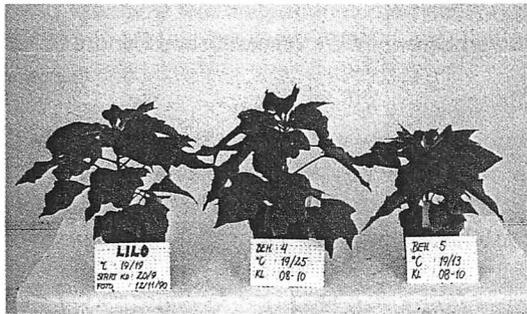


Fig. 4. Poinsettia plants, cultivar Starlight, grown at 19°C constant (left), at a 2-hour temperature increase to 25°C (middle) and a drop to 13°C for the first two hours of the day.

increase in temperature during the photoperiod may increase plant height and internode length and the effect seems to be about the same during the entire photoperiod (Erwin and Heins, 1995).

In some SDP, such as poinsettia and *Begonia*, plants show a change in sensitivity to Drop during the scotoperiod (dark period, Fig. 3).

Thus, Drop during the last two hours of the night period controlled plant height satisfactory in poinsettia plants (Fig. 4), and it is usually easy to accomplish in the greenhouse in the fall of cool climates due to low natural night temperature. The effect of Drop was rather small on time to flower as long as the ADT is maintained.

The differential sensitivity of stem elongation to temperature within the photo- and scoto-period may be controlled by an endogenous growth rhythm. A circadian (ca. 24 hours) growth rhythm was identified in *Dendranthema grandiflora* (Tutty et al. 1994) and *Campanula isophylla* (Torre and Moe, 1998). Plant stem elongation is not constant during a 24-h light and dark cycle. Both SDP and LDP grown under condition inductive for flowering elongate more rapidly during the night than the day (Torre and Moe, 1998; Erwin and Heins, 1995). High temperature during the

United States) during the 24-h daily growth cycle, generally at or just before first light of day. The responsiveness to temperature changes seems to be strongest during the first hours of the photoperiod (light) in both LDP, SDP and DNP and the cool morning drop is recommended for some plant species such as poinsettia, *Lilium longiflorum*, tomato, *Begonia x hiemalis* (Myster and Moe, 1995). A temperature drop of 6-8°C seems to have little retarding effects in many plant species. However, increasing the duration of the Drop treatment in the LDPs *Campanula isophylla* and *Fuchsia x hybrida*, results in greater inhibition of stem elongation. Ueber and Hendriks (1992, see also Jennerich and Hendriks 1997) reported that a much larger Drop (about 16°C) at dawn to 2-8°C for two hours reduced plant height up to 50% compared to the control plants in *Fuchsia x hybrida*, seed geranium and poinsettia. An

day applied as positive DIF, or as a short temperature increase, enhanced stem elongation, while a temperature increase at the beginning or end of the night did not affect *Salvia* and *Petunia* final internode length. In contrast Drop treatments reduced plant elongation when applied at the end of the scotoperiod in SDP poinsettia and begonia (Myster and Moe 1995, Myster 1999) when the stem elongation rate is high. Negative DIF application resulted in an overall reduction in stem elongation both in the photoperiod and the scotoperiod. This may indicate that negative DIF or Drop has an overall effect on inhibition of stem elongation by dawn regulation of bioactive GA₁. Also diurnal differences in elongation rate may be related to changes in GA activity and/or GA sensitivity during the 24-h day/night cycle. To our knowledge, no data are available to prove this hypothesis.

Some examples of application of DIF and Drop in practice

Four different temperature strategies for height control (limiting elongation) are now in commercial use by the greenhouse growers; Constant temperature, DIF, Drop, and a combination of DIF and Drop. DIF/Drop recommendation to various crops is based on experiments conducted over the last 15 years in the US, Europe and Japan. We present a few examples of using the DIF/drop concepts to some important crops (Fig. 5). For further information we recommend review articles of Myster and Moe (1995, 1997), Erwin and Heins (1995), Jennerich and Hendricks (1997) and Erwin (1998).

Constant temperature concept:

Many species grow considerably shorter when grown at constant temperature than

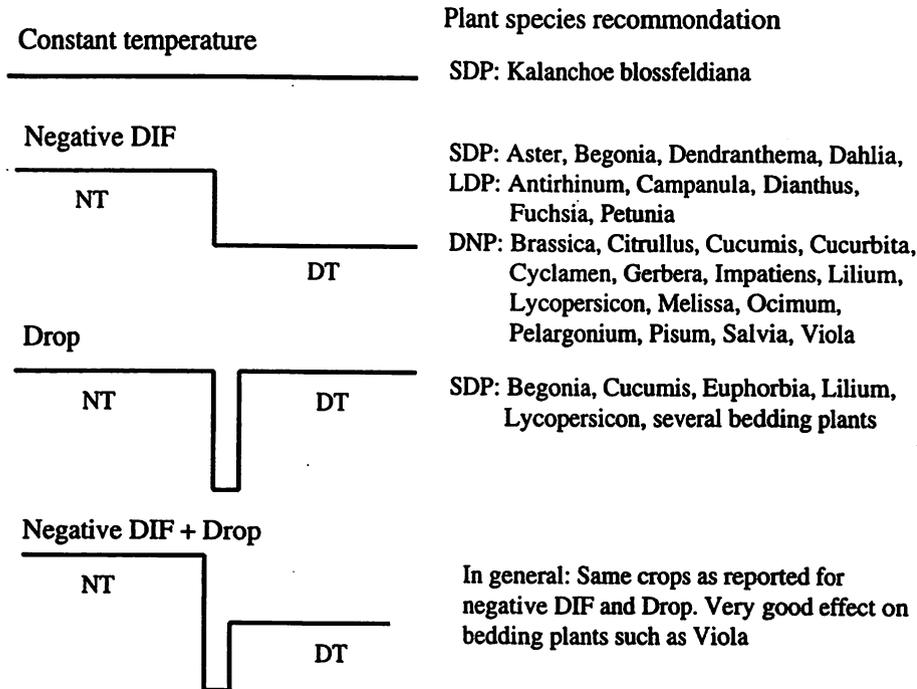


Fig. 5. Examples of using different temperature strategies for height control in some important greenhouse crops. SDP = short day plants, LDP = long day plants, DNP = day neutral plants.

at higher DT than NT (positive DIF). *Kalanchoe blossfeldiana* is the only pot species observed to date that becomes more compact when grown at constant temperature. Negative DIF and positive DIF enhance stem elongation and result in taller plants (Mortensen 1994).

Negative DIF concept:

A wide range of species among SDP, LDP and DNP respond very strongly to a lower DT than NT (Myster and Moe 1995, 1997), and negative DIF is applied to many important greenhouse crops. Some species do not respond to negative DIF including *Tulipa*, *Narcissus*, and tropical foliage plants. Erwin (1998) hypothesized that species indigenous to tropical environments are less sensitive to DT/NT than species from temperate and prairie environments.

Drop concept:

A limited number of species respond adequately to Drop and practical application has been successful so far in a few species including tomato, cucumber, poinsettia and *Begonia*, that is mainly SDP. However, the response of Drop in some bedding plants including both LDP and DNP, seems to be dependent on a very large Drop to 2-4°C. The very low temperature requirement may limit the use of very strong Drop due to problems of obtaining such a low temperature in the morning in the greenhouse.

Combination of DIF and Drop:

This temperature strategy has been applied successfully to several bedding plants, such as *Viola x wittrockiana* (pansy) and pot plants, such as *Dendranthema* and poinsettia (a small negative DIF plus 6-7°C Drop).

When DIF/Drop treatments were implemented in practice, the results sometimes were not as good as expected according to results from experiments. Jennerich and Hendriks (1997) have summarized some reasons for poor responses to DIF/Drop:

- Temperature reduction during the day is not possible due to high outdoor temperature.
- The temperature drop did not last long enough or was too small.
- Poor control of real air temperature and temperature regulation in the greenhouse.
- DIF/Drop treatments started too late in the culture.
- The plant species has a small response to DIF/Drop
- Cultivars under trial have a small elongation capacity (dwarf cvs)
- High plant density, high air humidity, or high N-supply
- High water supply

Interaction between DIF/Drop and light:

DIF and Photoperiod:

Photoperiod interacts with DIF to affect stem elongation and plant height. In general, the internode extension growth responses to DIF decrease as length of photoperiod increases (Erwin et al. 1991). The relative reduction in stem length in pea plants by negative compared to positive DIF decreased from 44 to 30 % as day-length increased from 10 to 14-h. (Grindal 1997). Many species grown under natural long days during summer in Northern Europe, show less response to negative

DIF than the response of the same species in the United States (Hendriks 1991, Vogelezang et al. 1992). These differences in DIF responses between locations are probably related to lower irradiance level or longer photoperiods compared with those present during experiments conducted in the United States (Erwin and Heins 1995). When the LDP spinach is transferred from SD to LD, it leads to an increase in GA_1 and Zeevaart et al. (1993) concluded that GA_1 is the primary active gibberellin for LD-induced stem elongation in spinach. Therefore, plants grown in longer photoperiods may produce high amount of GAs, which may limit the negative DIF response.

DIF/Drop and light intensity:

Mortensen and Moe (1992) showed that Drop treatments did not affect stem elongation in several plant species including *Begonia x hiemalis* under 16-h photoperiod. The results may be partly explained by irradiance level. They grew the plants under low irradiance of $80 \mu\text{molm}^{-2}\text{s}^{-1}$ for 16 h per day with fluorescent lamps. Recently, Myster (1999) reported that increasing photoperiod from 8 to 16 h to *Begonia x hiemalis* did not reduce the effect of Drop on plant height under higher irradiance level. Under low irradiance level, the effect of Drop was negligible under both short and long days. Also irradiance interacts with DIF to affect stem elongation (Erwin et al. 1992). Stem elongation responses to DIF increase as irradiance level increase and Erwin and Heins (1995) concluded that the basis for the increase in response of stem elongation to DIF as irradiance increases, is not understood. One hypothesis associated with the poor effect of negative DIF or Drop under low irradiance level is the lack of carbohydrate supply to the apex and the elongating internodes. For instance, Kristoffersen (1963) reported that the growth rate in tomato plants in the dark period increased with increasing irradiance during the previous day. Following a day with poor light condition, tomato plants elongate very little the following day (Bertram 1992). Under such condition, we may not expect much response to a Drop/DIF treatment.

DIF/Drop and light quality:

Experiments on *Campanula isophylla* demonstrated a clear interaction between light quality, DIF, and stem elongation (Moe et al. 1991). Continuous far-red (FR) light or incandescent light of a low R/FR ratio almost nullified the negative DIF reduction in stem elongation on *Campanula* (Moe et al. 1991), *Fuchsia* (Erwin and Heins, 1995), and pea (Grindal 1987). Wild type cucumber grown with a R light day extension, developed about 60 % shorter internodes and 40 % shorter hypocotyls and petioles under negative than positive DIF. A 30-min end-of-day (EOD) FR treatment increased elongation growth and decreased the inhibitory effect of negative DIF. Phytochrome B is thought to partly mediate increase in stem elongation in response to EOD-FR treatment in light grown plants (Smith and Whitelam 1997). Our EOD-FR experiments with pea and cucumber also indicate that negative DIF response is enhanced when the phytochrome is converted to the active Pfr form at the end of the day and/or during the night.

An interaction between DIF and light quality established with selective plastic films during the photoperiod is also reported for some plant species (see Grindal et al., page 75). Experiments with *Fuchsia* and *Petunia* grown under R/FR ratios of 0.7 (SXE-4), 1.1 (clear plastic) and 1.6 (YXE-10) showed that the effect of DIF was

relatively stronger under plastic film with a high compared with the one with a low R/FR ratio (Grindal et al. 2000). In contrast, the response pattern is opposite in cucumber where the response to light quality is stronger under positive than negative DIF. Daylight supplemented with R light enhanced the inhibition of *Fuchsia* stem elongation to a negative DIF environment (unpublished data, Erwin and Heins, 1995), and they hypothesize that phytochrome photoequilibrium or cycling and DIF affect stem elongation using a similar pathway.

The effect of blue light on plant responses to DIF is not determined.

Preliminary data suggest that supplemental blue lighting during the day, reduces stem elongation in general but does not interact with DIF to reduce stem elongation. Maas and Hattum (1998) reported that *Fuchsia* plants grew tall due to lack of blue light, and were not much affected by DIF compared with plants grown under white light with the same R/FR ratio.

Experiments with phytochrome A and B mutants and cryptochrome (cry 1 and cry 2) mutants in *Arabidopsis* show negative DIF responses in phytochrome A and both cryptochrome mutants, while the response of phy B mutants is minor (R. Moe and R. E. Kendrick, unpublished data). Experiments with a phytochrome B deficient cucumber mutant, lh, showed no effect of negative DIF on hypocotyls elongation (Grindal et al., page 65). Recently, Runkle and Pearson (1998) concluded that phytochrome A did not mediate reduced stem extension from negative DIF/Drop treatments in tomato and potato plants. Taken all available information together, the results may indicate that phy B is involved in both thermo- and photomorphogenic control of elongation growth.

Thermomorphogenesis induced by DIF/Drop is in many cases similar to photomorphogenesis induced by light quality (Moe and Heins, 1990). They suggest that DIF in some way has an influence on phytochrome action. The responses of plants to a low R/FR photon ratio or to FR enriched light are similar to the response of plants to a positive DIF. On the other hand, the responses of a plant to a high R/FR ratio or to R light are similar to responses of plants to negative DIF (Table 1). However, the physiological basis for DIF and light quality elicited stem elongation responses seem not to be identical. It is evident that negative DIF induced inhibition of stem elongation is related to reduced bioactive GA₁ content in the plant tissue (Grindal et al., page 65). The involvements of phytochrome are not clear, but active Pfr seems to be required for proper negative DIF response. Light quality effects on stem elongation act through both influences on phytochrome status and changes in tissue sensitivity to GAs. Depletion of Pfr by FR exposure in *Cucumis sativum* increased tissue responsiveness to exogenous gibberellin application (Lopez-Juez et al. 1995). Additional evidence provided by Ross and Reid (1992) show that EOD-FR treatment, which enhanced stem elongation in pea, did not affect endogenous GA₁ level.

It is likely that phytochrome photoequilibrium and GA levels act on stem elongation through the regulation of different partial processes when light quality and DIF are applied. FR light seems to increase tissue sensitivity to GA and not GA metabolism. In contrast some results in pea, *Dendranthema*, and *Fuchsia* indicate that tissue sensitivity to GA was not influenced by DIF but played a significant role in the control of the level of bioactive GA₁ (Grindal et al. 1998).

Table 1. Comparison of photo- and thermomorphogenesis in greenhouse plants mediated by light quality and DT/NT alternations (DIF). R = red light, FR = far red light, DIF = difference

between day and night temperature, - DIF = negative DIF, + DIF = positive DIF, - means retardation, + means promotion (modified after Moe and Heins, 1990).

Plant responses	R	FR	-DIF	+DIF
Stem elongation	-	+	-	+
Petiole elongation	-	+	-	+
Peduncle elongation	-	+	-	+
Leaf orientation				
Upright	-	+	-	+
Downwards	+	-	+	-
Lat. branching	+	-	(+)	(-)
Leaf coloring (red)	+	-	+	-
Leaf chlorosis	-	+	+	-

DIF/Drop and postharvest life

The stem dry weight of *Impatiens* and *Fuchsia* plants increased linearly as DIF increased from -10 to +15°C, and percent partitioning of dry weight into stems versus flowers and leaves depended primarily on DT (See Erwin and Heins 1995). Also *Begonia x hiemalis* grown under different DIF regimes ranging from -9 to +9°C, showed that percent shoot and leaf dry weight was lower in plants grown at negative DIF than in plants grown at zero or positive DIF. However, keeping quality of plants was not affected by DIF (Willumsen et al. 1995). Studies in *Lilium longiflorum* showed that carbohydrate content decreased as DIF decreased (Miller et al. 1993) and the postharvest life was significantly reduced only when plants were grown in an environment with a DT considerably lower than the NT. *Cyathia* abscission occurred more quickly on negative DIF than positive DIF grown poinsettia plants (Moe et al. 1992). With drop treatment, postharvest problems seem to be minor in poinsettia (personal observations). The influence of diurnal temperature treatments during poinsettia production had no significant influence on postharvest susceptibility of poinsettia bract and foliage to *Botrytis cinerea* (Pritchard et al. 1996). Results suggested that commercial growers using higher NT than DT to control plant height are not increasing the risk for *B. cinerea* infection during postharvest handling. In *Campnula* postharvest life was even longer for negative DIF than positive DIF grown plants (Serek 1991). When the plants are grown under poor light conditions, the negative DIF treatment may result in reduction in postharvest life due to less assimilate supply to the roots and flowers (Hendricks, personal communications). For instance, higher irradiance to Christmas begonia during the production phase enhanced keeping quality and flower bud opening/growth during the postharvest period in interior room with low light level (Fjeld 1989). The impact of negative DIF/Drop should be studied in more details to understand the involvement of the treatments on postharvest life in different crops. DIF/Drop and graphical tracking.

DIF/Drop and graphical tracking

Graphical tracking is a term used for a decision-support procedure whereby actual plant height is measured and plotted on a graph to compare the actual height with that expected according to a predetermined growth curve. The use of graphical tracking is based on: 1) the ability to predict desired plant height during development, 2) measurements at intervals of actual plant height and plotting of information on a graph to compare with predicted height, and 3) the possibility to adjust the temperature, apply growth retardants, or otherwise affect stem elongation in order to minimize the difference between actual and expected plant height at any time during the growing period (Heins et al. 1988). Based on findings in Michigan

(Heins et al. 1988) and Norway (Moe 1993) graphical tracking is commonly used for height control in poinsettia in many countries. A 2-hour Drop at the end of the night combined with some cycocel application has resulted in a substantial improvement of the plant quality. For further information about modelling of plant growth, see Snipen, page 150).

The correct graphical tracking curve has become more problematic for height control of newer poinsettia cultivars (Fisher and Heins, 1997). The original graphical tracking curve (Heins and Carlson, 1990) was developed with the rapidly elongating 'Annette Hegg' poinsettia cultivars. The new, short-growing cultivars, such as 'Freedom', have been a mixed blessing for growers. Shoots of such cultivars elongate slowly when plants are widely spaced, but these same shoots elongate rapidly when the crop canopy closes. Canopy closure typically occurs after first bract coloration, at a time when applications of growth retardants reduces bract expansion. DIF and DROP are very effective tools for height control following canopy closure as long as day temperatures can be adequately controlled. Unfortunately, day temperature often cannot be controlled due to high outside temperatures and high solar radiation; This results in unacceptable stem elongation. If the grower anticipates this increase in elongation and keeps plants short, and the crop matures before canopy closure, the crop never reaches desired height. If the grower allows the crop to elongate to near final height not anticipating this final elongation, and the elon-

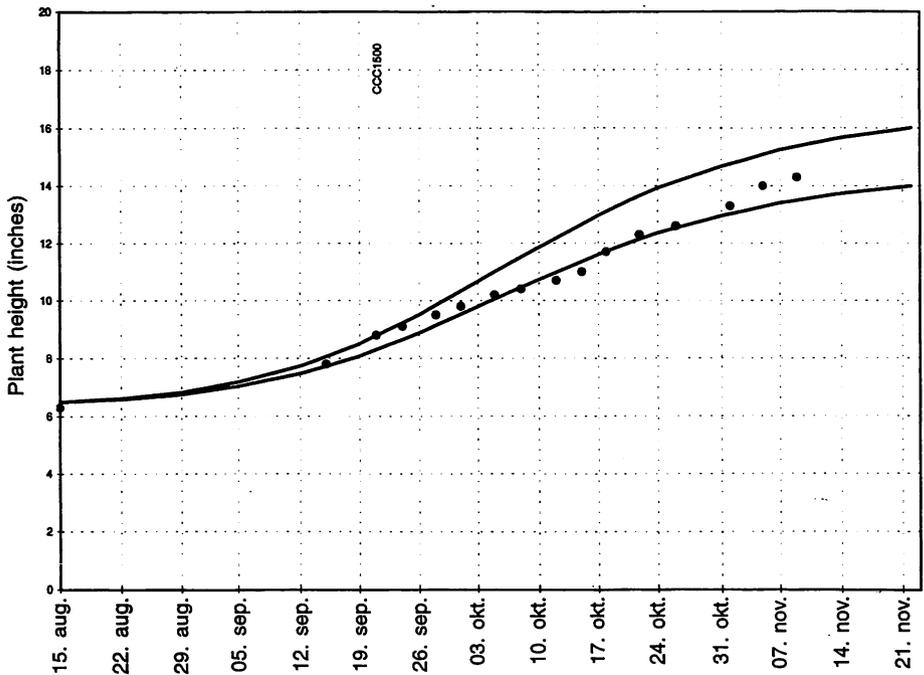


Fig. 6. Graphical tracking for poinsettia, cv. Freedom Red, developed by Paul Fischer, Dept. of Plant Biology, University of New Hampshire, USA, 1997. The following information was plotted for making the graphical tracking: Pot size: 15 cm (6 inches), Date for start of crop: August 15, Date for flower initiation: September 23, Date for marketing: November 25, Response time: 9 weeks, Plant height at start : 16 cm (6,5 inches), Final desired minimum plant height: 35 cm (14 inches), Final maximum plant height: 40 cm (16 inches). The plants were, as indicated, sprayed with CCC (1500 ppm) on September 21. The dots show the actual plant height as measured during the growing period.

gation occurs under natural positive DIF conditions, the crop grows excessively tall. A reliable method to control elongation without adversely affecting bract size is yet to be found.

A successful use of graphical tracking for the cultivar Freedom Red is shown in Fig. 6. Only one spray of chlormequat (CCC) was required to control the plant height within the desired plant height between 35 and 40 cm when proper DIF treatments were applied.

Graphical tracking has become a standard cultural method in the production of Easter lilies in the United States (Heins, et al, 1987). Because Easter lily is produced mainly during the coolest part of the year, DIF and DROP are the major height-control tools used by growers in the northern United States. Growth retardants such as ancymidol and uniconazole augment negative DIF and DROP, especially as the season progresses and as plants are produced in progressively warmer climates.

Stem elongation models have been developed for graphical tracking of other crops such as geranium (Fisher, et al, 1998), Oriental lily, and hybrid lily (Fisher et al, 1998). Use of DIF has become a standard height-control strategy for these crops using graphical tracking as a basis for decision support.

References

- Bertram, L. 1992. Stem elongation of *Dendranthema* and tomato plants in relation to day and night temperature regime. *Acta Hort.* 327:61-70.
- Erwin, J. E. 1998. Temperature and light effects on stem elongation. *J. Japan. Soc. Hort. Sci.* 67 (6):1113-1120.
- Erwin, J. and Heins, R. D. 1995. Thermomorphogenic responses in stem and leaf development. *HortScience*, 30(5):940-949.
- Erwin, J. E., Heins, R. D. and Karlsson, M. G. 1989. Thermomorphogenesis in *Lilium longiflorum* Thumb. *Amer. J. Bot.* 76:47-52.
- Erwin, J. E., Heins, R. D., Carlson, W. and Newport, S. 1992. Environmental and mechanical manipulation of stem elongation. *PGRSA Quart.* 20:1-17.
- Fisher, P. R. and R. D. Heins. 1997. From first color to flower. *Greenhouse Grower* 15(12):27-28.
- Fisher, P., Heins, R. D., Liu, B. and Bilodeau, L. 1998. Tracking Oriental and Hybrid Lilies. *Greenhouse Grower.* 16(1):39-40.
- Fisher, P. R., Heins, R. D., Smith, B. and Chong, J. 1998. Tracking geraniums. *Greenhouse Grower* 16(8):79-80.
- Fjeld, T. 1989. Studies on factors affecting the keeping quality of Christmas begonia (*Begonia cheimantha* Everett). Dr. Scient. Thesis 1989:16 at the Agricultural University of Norway.
- Grindal, G. 1997. Thermoperiodic stem elongation in *Pisum sativum* L. and *Cucumis sativus* L. – the role of gibberellins and phytochrome. Dr. Scient. Thesis 1997:27 at the Agricultural University of Norway.
- Grindal, G. Ernstsens, A., Reid, J. B., Junttila, O., Lindgård, B. and Moe, R. 1998. Endogenous gibberellin GA₁ levels control thermoperiodic stem elongation in *Pisum sativum*. *Physiol. Plant.* 102:523-531.

- Grindal, G., Oi, R., Gissinger, A. and Moe, R. 2000. Plant morphology is affected by light quality selective plastic films and alternating day and night temperature. *Scientia Hort.* (accepted for publication).
- Heins, R. D. and Carlson, W. H. 1990. Understanding and applying graphical tracking. *Greenhouse Grower* 8(5):73-80.
- Heins, R. D., J. Erwin, M. Karlsson, R. Berghage, W. Carlson, and J. Biernbaum. 1987. Easter lily responses to temperature during forcing, II. Tracking Easter lily height with graphs. *GrowerTalks* 51(8):64, 66, 68.
- Heins, R. D., Erwin, J., Berghage, R., Karlsson, M., Biernbaum, J. and Carlson, W. 1988. Use of temperature to control plant height. *Greenhouse Growers* 6 (9):32-34.
- Hendriks, L. 1991. Diff bei Beet- und Balkonpflanzen. *Gb+Gw* 39:1883-1889.
- Jennerich, L. und Hendricks, L. 1997. *Temperaturregelstrategien*. Bernhard Thalaker Verlag GmbH & Co. KG, Braunschweig. 167 pp.
- Kristoffersen, T. 1963. Interactions of photoperiod and temperature in growth and development of young tomato plants. *Physiol. Plant. Suppl.* 1:1-98.
- Lopez-Juez, E., Kobayashi, M., Sakurai, A., Kamiya, Y. and Kendrick, R. E. 1995. Phytochrome, gibberellins, and hypocotyl growth. *Plant Physiol.* 107:131-140.
- Maas, F. M. and Hattum, J. van, 1997. The role of gibberellins in thermo- and photocontrol of stem elongation in *Fuchsia*. *Acta Hort.* 435:93-104.
- Miller, W. B., Hammer, P. A. and Kirk, T. I. 1993. Reversed greenhouse temperature after carbohydrate status in *Lilium longiflorum* Thunb. 'Nellie White'. *J. Amer. Soc. Hort. Sci.* 118:736-740.
- Moe, R. 1990. Effect of day and night temperature alternations and plant growth regulators on stem elongation and flowering of the long-day plant *Campanula isophylla* Moretti. *Sci. Hort.* 43:291-305.
- Moe, R. 1994. Morphogenetic effects of temperature and the control of plant height by day/night temperature alternations. In: E. Strømme, ed. *The scientific basis of poinsettia production*. The Agricultural University of Norway, Advisory Service, Aas, Norway, Chapter 9, pp 65-72.
- Moe, R. and Heins, R. D. 1990. Control of plant morphogenesis and flowering by light quality and temperature. *Acta Hort.* 272:81-89.
- Moe, R., Heins, R. D. and Erwin, J. 1991. Stem elongation and flowering of the long-day plant *Campanula isophylla* Moretti in response to day and night temperature alternations and light quality. *Scientia Hort.* 48:141-151.
- Moe, R., Fjeld, T. and Mortensen, L. M. 1992. Stem elongation and keeping quality in poinsettia (*Euphorbia pulcherrima* Willd.) as affected by temperature and supplemental lighting. *Scientia Hort.* 50:127-136.
- Mortensen, L. M. 1994. Effects of day/night temperature variations on growth, morphogenesis and flowering of *Kalanchoe blossfeldiana* v. Poelln. at different CO₂ concentrations. *Scientia Hort.* 59:233-241.
- Mortensen, L. M. And Moe, R. 1992. Effects of various day and night temperature treatments on morphogenesis and growth of some greenhouse and bedding plant species. *Acta Hort.* 327:145-153.
- Myster, J. 1999. The effects of temperature alternations, irradiance level, photoperiod, and day extension light quality on morphogenesis, growth and flowering of *Begonia x hiemalis* Fotsch. *Gartenbauwissenschaft* 64 (5): 206-213.
- Myster, J. and Moe, R. 1995. Effect of diurnal temperature alternations on plant morphology in some greenhouse crops – a mini review. *Scientia Hort.* 62:205-215.

- Myster, J und Moe, R. 1997. Diff und Drop in Skandinavien – Versuche und praktische Anwendung. p. 83-96. In: L. Jennerich and L. Hendricks. Temperaturregelstrategien. Bernhard Thalacker Verlag.GmbH & KG, Braunschweig. 167 pp., 1997.
- Pritchard, P. M., Hausbeck, M. K. and Heins, R. D. 1996. The influence of diurnal temperatures on the postharvest susceptibility of poinsettia to *Botrytis cinerea*. Plant Dis. 80:1011-1014.
- Ross, J. J. and Reid, J. B. 1992. Ontogenetic and environmental effects on GA₁ levels and the implications for the control of internode length. p. 180-187. In: C. M. Karssen, Van Loom L. C. And D. Vreugdenhil (eds.). Progress in plant growth regulation. Kluwer Academic Publishers, Boston, MA.
- Runkle, E. and Pearson, S. 1998. Phytochrome A does not mediate reduced stem extension from cool day-temperature treatments. Physiol. Plant. 104:596-602.
- Serek, M. 1991. Post-harvest characteristics of *Campanula carpatica*: Influence of temperature programming. Gartenbauwissenschaft 56:71-74.
- Smith, H and Whitelam, G. C. 1997. The shade avoiding syndrome: multiple responses mediated by multiple phytochromes. Plant Cell Environ. 20:840-844.
- Strøm, M. and Moe, R. 1997. DIF affects internode and cell extension growth and cell number in *Campanula isophylla* Moretti. Acta Hort. 435:17-24.
- Tangerås, H. 1979. Modifying effects of ancymidol and gibberellins on temperature induced elongation in *Fuchsia x hybrida*. Acta Hort. 91:411-417.
- Torre, S. and Moe, R. 1998, Temperature, DIF and photoperiod effects on the rhythm and rate of stem elongation in *Campanula isophylla* Moretti. Scientia Hort. 72:123-133.
- Tutty, J. R., Hicklenton, P. R., Kristie, D. N. and McRae, K. B. 1994. The influence of photoperiod and temperature on the kinetics of stem elongation in *Dendranthema grandiflorum*. J. Amer. Soc. Hort. Sci. 119:138-143.
- Ueber, E. and Hendriks, L. 1992. Effect of intensity, duration and time of a temperature drop on growth and flowering of *Euphorbia pulcherrima* Willd ex Klotzsch. Acta Hort. 327:33-37.
- Vogelezang, J., Moe, R., Schüssler, H., Hendricks, L., Cuijpers, L. and Ueber, E. 1992. Cooperative European research on temperature strategies for bedding plants. Acta Hort. 327:11-16.
- Went, F. W. 1944. Plant growth under controlled conditions. II. Thermoperiodicity in growth and fruiting of a tomato. Am. J. Bot. 31:135-150.
- Willumsen, K., Fjeld, T. and Moe, R. 1995. The effects of different day and night temperature regimes on growth, flowering, and keepability of *Begonia x hiemalis* Fotsch. Gartenbauwissenschaft 60:167-170.
- Zeevaart, J. A. D., Gage, D. A. and Talon, M. 1993. Gibberellin-A₁ is required for stem elongation in spinach. Proc. Nat. Acad. Sci. USA, 90:7401-7405.