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Stem elongation and flowering of the long-day plant *Campanula isophylla* Moretti in response to day and night temperature alternations and light quality

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ABSTRACT

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Stem elongation and plant height at flowering in *Campanula isophylla* Moretti were greater when plants were exposed to far red (FR) light or light from incandescent lamps which had a low red (R)/FR ratio (0.7). The difference in final stem length between FR- and R-light-treated plants was greatest when the light treatments were given during the entire night or as a 3 h end-of-day (EOD) lighting period. Only minor differences existed between R and FR light treatments when plants were given light in the middle of the night. However, FR light suppressed lateral branching compared with R light. The reduction in plant height as a result of a lower day temperature (DT) than night temperature (NT) was nullified by day-extension lighting with incandescent lamps. With fluorescent lamps (R/FR ratio 4.2), plant height was significantly less at 15/21°C (negative DT-NT (DIF)) than at 21/15°C DT/NT (positive DIF). Continuous lighting (CL) during the entire night or with 3 h night interruption (NI) treatments with R or FR light immediately after the middle of the night was equally effective at inducing flowering, and much more effective than EOD or end-of-night (EON) lighting. DIF had a slight influence on the rate of flower development, but negative DIF grown plants had 24% more flowers and flower buds, and 26% higher dry weight, than positive DIF plants. Practical applications of light quality and negative DIF treatments for the production of high-quality pot plants of *C. isophylla* are discussed.

Keywords: *Campanula isophylla*; flowering; lateral branching; light quality; long-day plant; night interruption; stem elongation; temperature; thermomorphogenesis.

Abbreviations: ADT = average daily temperature; CL = continuous lighting; DIF = difference between DT and NT (DT − NT); DT = day temperature; EOD = end-of-day; EON = end-of-night; FR = far red; LD = long day(s), LDP = long-day plant(s): NI = night interruption; NT = night temperature; PAR, photosynthetically active radiation; Pfr = far-red-absorbing form of phytochrome; R = red; SD = short day(s); VB = visible bud.

INTRODUCTION

Campanula isophylla Moretti is a long-day plant (LDP) which has become of considerable commercial importance as a flowering pot plant or hanging basket plant for indoor and outdoor use. With day length extension applied from early December, the plants start to flower in early spring (Moe and Heide, 1985). The plants are generally marketed when they have 20–30 open flowers and more than 50 flower buds; the total plant height should not exceed 25 cm. Excessive internode elongation is difficult to control in *Campanula* when the plants are grown under a standard temperature regimen with a higher day temperature (DT) than night temperature (NT). Recently, Moe (1990) showed that stem elongation in *C. isophylla* is influenced more by the difference between DT and NT (DT − NT = DIF) than by average daily temperature (ADT) or absolute DT and NT. Similar thermomorphogenic responses to DIF have been reported in other LDP such as *Lilium longiflorum* (Erwin et al., 1989), *Fuchsia × hybrida* (Tangerås, 1979) and *Dianthus* (Moe, 1983).

Plant height of *Campanula* is reduced by growth retardant applications; daminozide (Alar) is frequently used in practice. However, the use of daminozide or other growth retardants has to be restricted because of the risk of environmental pollution. It is, therefore, necessary to find alternative treatments for controlling plant height. One possibility is to change the growth temperature to a lower DIF level or to DT < NT (Moe and Heide, 1985; Moe, 1990). Another possibility is to change the lighting strategy in such a way that stem elongation could be suppressed without delaying flowering. Internode elongation in many plant species is affected by light quality during the day and/or the night. The ratio of the red (R) and far red (FR) absorbing form of the phytochrome, established by artificial lighting with lamp types of different spectra (Cathey and Campbell, 1979; Grimstad, 1981; Tibbits et al., 1983), by selective screening of the natural light spectrum (Mortensen and Strømme, 1987), or by shadelight (Morgan and Smith, 1981) strongly affects stem elongation and lateral branching. Lighting some LDP throughout the night using incandescent lamps (low R/FR ratio) results in the inhibition of lateral branching and promotes internode growth (Downs et al., 1958; Moe and Holmenlund, 1989). Exposure of the LDP *Fuchsia × hybrida* to end-of-day (EOD) irradiation from fluorescent lamps (high R/FR ratio) decreased internode elongation (Vince-Prue, 1977), but flowering seems to depend on exposure to a long photoperiod with more or less continuous lighting (Vince-Prue, 1983). The results with *Fuchsia* indicate that the selection of a lamp type with high amounts of R light and continuous lighting (CL) may be beneficial for controlling both plant morphogenesis and flowering in the LDP *C. isophylla*.

The objectives of this research work were to (1) identify light quality treat-

ments which could control stem elongation without delaying flowering and without suppressing lateral branching, and (2) discover whether light quality interacts with DIF in the control of stem elongation and flowering.

MATERIALS AND METHODS

Experiment 1: Effect of R and FR light. – Ten-week-old vegetatively propagated plants of *C. isophylla* cultivar 'Blå' (blue cultivar from the Skjold nursery, Norway) were obtained from a commercial propagator and potted in 11 cm plastic pots. The growing medium was fertilized Norwegian peat moss (Floralux). The plants were watered with a 14.3 mM N, 1 mM P and 5.1 mM K nutrient solution, and grown at 18°C for 7 days in a glasshouse under non-inductive day-length (12 h) until the start of the experiment. Plants were then placed in growth rooms at 18 ± 0.5°C with a water vapor deficit of 660 ± 66 Pa. All plants were irradiated for 12 h day^{-1} at 69 μmol s^{-1} m^{-2} from cool white fluorescent lamps (Philips TL 33). The photosynthetic photon flux density was measured with a Lambda Li-Cor, Inc., instrument, Model 1-185 B.

The 12 h day was extended by including a 12 h dark period (short day (SD) control), a low irradiance of R or FR light applied throughout the entire 'night', or a 3 h EOD (EOD 0–3 h), night interruption (NI, 4–6 or 7–9 h) or end-of-night (EON, 10–12 h) treatment. The day–night transition was conducted at time 0 h. R light was provided by 40 W red fluorescent lamps (Philips TL 15) with a maximum output at 660 nm (Fig. 1). FR light was

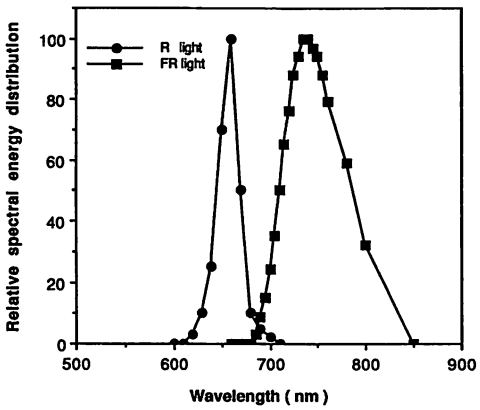

Fig. 1. Relative spectral energy distribution of R and FR light sources measured using a UDT 11 D Spectroradiometer scanning from 390 to 1100 nm. The R light source was 40 W red fluorescent lamps (Philips TL 15). The FR light source was 60 W incandescent lamps screened with one layer of 3 mm red plexiglass (No. 501) and two layers of 3 mm blue plexiglass (No. 627) from Røhm and Haas, Germany.

obtained by filtering from 60 W incandescent lamps with one layer of 3 mm red plexiglass (No. 501) and two layers of 3 mm blue plexiglass (No. 627) from Røhm and Haas, Darmstadt, Germany. The maximum output was at about 735 nm (Fig. 1). The irradiances at plant level under R and FR lights were 0.25 W m^{-2} and 0.15 W m^{-2} (400–1000 nm), respectively. These measurements were carried out with a UDT 11A Radiometer for total irradiance and with a UDT 11D Spectroradiometer for spectral scanning from 390 to 1100 nm. Five plants were used in each treatment group and the experiment was replicated twice.

Experiment 2: Effect of light quality and DT/NT alternations. – The same plant material and pre-treatments as described in Experiment 1 were used. After 1 week of growth under 12 h SD, the plants were placed at 21/15°C DT/NT (positive DIF) or 15/21°C DT/NT (negative DIF) in combination with fluorescent lamps or incandescent lamps as a 14 h day extension to provide CL for flowering. All plants were irradiated daily for 10 h with cool white fluorescent lamps at a photosynthetic photon flux density of 69 μmol s^{-1} m^{-2} photosynthetically active radiation (PAR) (3.98 mol day^{-1} m^{-2}) at plant level; this light period is here called 'day'. To establish different phytochrome photoequilibria (Pfr/Ptotal, where Pfr is the far red absorbing form of phytochrome) during the 14 h 'night', the day was extended with a low irradiance of 0.58 W m^{-2} (400–1000 nm), either from fluorescent lamps (Philips SL 18 W) high in R light (R/FR ratio of 4.2) or from incandescent lamps high in FR light (R/FR ratio of 0.7). R/RF ratios were determined by measuring the energy output at 660 and 730 nm, respectively, with a Li-Cor, Inc., instrument. The changes from DT to NT and vice versa were synchronized with the shifts from photosynthetic (69 μmol s^{-1} m^{-2}) to low photoperiodic irradiation. Each treatment consisted of five plants and the experiment was replicated twice.

Data and statistical treatments. – Stem length was measured weekly from the start of the experiments to anthesis or for at least 12 weeks on the SD control plants and on plants in treatments where flower induction was severely delayed. The longest shoot was measured on each plant. The number of days to visible bud (VB) and to first open flower (anthesis) were recorded. In addition, the number of flowers opened per plant was recorded at the termination of Experiment 1, 17 weeks. In Experiment 2, total number of flowers and flower buds was recorded at the termination of the experiment. Plant dry weight was measured at the end of Experiment 2 after the plant materials had been dried for 3 days in an oven set at 80°C. An analysis of variance on data was conducted according to standard procedures and a regression analysis was carried out using Cricket software, Great Valley Corporate Center, PA, USA.

RESULTS

Experiment 1: Effect of R and FR light. – Stem elongation and flower initiation were not affected in the same way by R and FR light. Continuous irradiation with R and FR light during the 12 h night period had an equal effect on the time from induction to VB (Fig. 2(B)). However, stem elongation was promoted 67% more with FR than with R light. Plants grown under SD conditions (12 h) grew vegetatively and elongated very slowly (Fig. 2(A)). A NI with FR light for 3 h before the middle of the night (Fig. 2(C)) resulted in delayed VB and a higher rate of stem elongation compared with plants exposed to R light. No significant ($P<0.05$) differences in elongation rate or flowering were observed when plants received either R or FR as NI lighting immediately after the middle of the night (Fig. 2(D)). EOD FR lighting promoted stem elongation compared with R light, but the growth rate was not as great as with continuous FR light (Fig. 2(E)). VB was delayed by about 4 weeks using EOD FR lighting as compared with using NI (7–9 h) or CL. Stem elongation and flowering responses to R and FR light were opposite when EON lighting (Fig. 2(F)) was applied compared with EOD lighting.

To separate the response of light quality from photoperiodic (flowering)-mediated stem elongation, the differences in stem length between FR- and R-light-treated plants, and R- or FR- and dark-treated plants after a 10 week growth period were calculated (Table 1). R light treatments (CL or NI) associated with early VB resulted in the same increase in stem length compared with the dark control, which grew vegetatively. However, EOD R light or EON FR light treatments, which both strongly delayed VB (see Fig. 2(E) and 2(F)), had almost the same stem length as the dark control (Table 1). FR light resulted in a large increase in stem length relative to R light when exposures occurred early in the night. As exposure to FR light occurred later in the night, the differences in stem length between FR and R light decreased, although the flowering response was about the same.

Plants grown under CL reached anthesis after 9.5 weeks. R and FR light had an equal effect on time to anthesis, but FR light resulted in 120 more flowers per plant (Table 2). R light was more effective than FR light in promoting flowering when given as a NI (7–9 h). EOD lighting was ineffective in promoting flowering. None of the plants had reached anthesis at 17 weeks of treatment. EON lighting with FR light was also ineffective in promoting flowering, but plants receiving EON R light reached anthesis after 14 weeks.

Lateral shoot development was inhibited by the light treatments during the night as the dark control plants had the greatest number of lateral shoots (Table 2). In general, FR light inhibited lateral branching more than R light. EOD and early NI exposure to FR light were more inhibitory than light treatments later in the night.

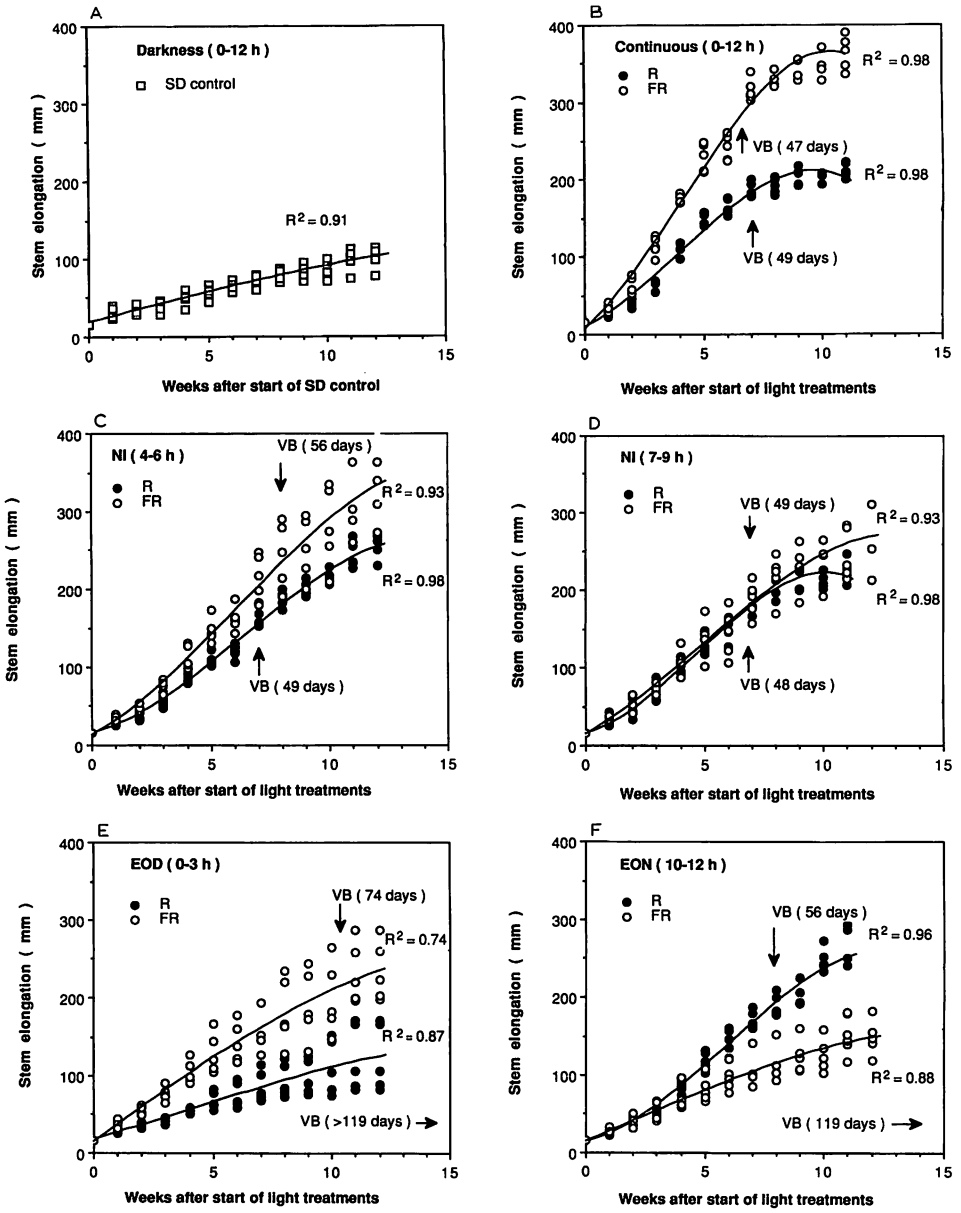

Fig. 2. Effect of SD (A) and of continuous (B) or 3 h (C–F) R or FR light treatments during the 12 h night on stem elongation and time to visible flower bud (VB) in *C. isophylla* 'Blå'. The R and FR light periods were applied as follows: NI = night interruption (C and D), EOD = end-of-day (E), EON = end-of-night (F). The time of day–night transition was set at 0 h. All plants were irradiated daily for 12 h with cool white fluorescent lamps with a photon flux density of 69 μmol s^{-1} m^{-2} PAR. The number of days to VB is indicated. Stem elongation, based on final height after a 10 week growth period, was significantly different ($P<0.01$) for R and FR light, except with the NI (7–9 h) treatment (non-significant at the 5% level).

TABLE 1

Effects of various R and FR light treatments given as continuous light (CL), night interruption (NI), end-of-day (EOD), end-of-night (EON) or darkness (D) during the night (12 h) on stem length (mm) and visible flower buds (VB) in *C. isophylla* 'Blå'. The differences in days from the start of treatment to VB, and stem length after a 10-week growth period between FR and R light (FR−R) and between FR and D (FR−D) or R and D (R−D) light, are given. The shift from day to night is set at time 0 h. Values within parameters followed by different letters are significantly different at the $P<0.05$ level according to Duncan's multiple range test

Light treatment	Difference in days to VB (FR−R)	Difference in stem length		Stem length increase of FR relative to R (%)
		FR−D (mm)	R−D (mm)	
CL (0–12 h)	−2 a	256.1 a	110.9 a	72.1 a
NI (4–6 h)	+7 b	189.9 b	124.7 a	30.3 b
NI (7–9 h)	+1 a	148.7 c	121.1 a	13.0 c
EOD (0–3 h)	> −45 c	110.2 d	21.3 c	79.5 d
EON (10–12 h)	+63 d	35.5 e	158.3 b	−49.4 e
D (0–12 h)	No VB			

TABLE 2

Effects of red (R) and far-red (FR) light after a 12-h day, applied as continuous lighting (CL) during the 12 h night or as a 3 h night interruption (NI), end-of-day (EOD) or end-of-night (EON) lighting, on the number of days from the start of treatments to anthesis, number of open flowers per plant after 17 weeks of growth and number of lateral shoots per plant in *C. isophylla* 'Blå'. The SD control plants were grown at a 12 h photoperiod. All plants were irradiated with 69 μmol s^{-1} m^{-2} PAR from fluorescent lamps during the 12 h day. The day–night transition was set at time 0 h. NI, EOD and EON lighting were applied for 3 h. > 119 days = no plants had reached anthesis when the experiment was terminated. Veg. = vegetative plants. Values within parameters followed by different letters are significantly different at the $P<0.05$ level according to Duncan's multiple range test.

Treatment during night	Days to anthesis		No. of flowers per plant		No. of lateral shoots per plant	
	R	FR	R	FR	R	FR
CL (0–12 h)	66.2 a	65.6 a	186.2 a	307.0 d	9.8 a	7.0 b
NI (4–6 h)	94.6 c	90.8 c	42.8 b	29.4 b	6.0 bc	3.8 d
NI (7–9 h)	74.0 b	94.4 c	189.4 a	32.6 b	9.2 a	4.6 c
EOD (0–3 h)	> 119 d	> 119 d	0 c	0 c	8.0 b	3.5 d
EON (10–12 h)	96.6 c	> 119 d	42.4 b	0 c	5.6 c	9.6 a
SD control	Veg.		Veg.		10.8	

Experiment 2: Effect of light quality and DT/NT alternations. – Neither day/night temperature alternations nor light quality delivered as day-extension light treatments influenced the number of days from the start of CL treat-

ments to VB (Table 3). Plants grown at negative DIF (15/21 °C) reached anthesis 3–4 days earlier and had on average 24% more flowers and flower buds per plant than plants grown with a positive DIF. DIF interacted with light quality to influence the total number of flowers and flower buds. With positive DIF, plants growing under fluorescent lamps had 25% more flowers and flower buds than plants growing under incandescent lamps. However, when plants were grown with negative DIF, the result was the opposite: plants growing under incandescent lamps had 14% more flowers and flower buds than plants growing under fluorescent lamps.

Day-extension lighting with incandescent lamps (R/FR=0.7) enhanced stem elongation more than lighting with fluorescent lamps (Table 3). Light quality interacted with DIF to affect stem elongation. When the plants were grown under fluorescent lamps (R/FR=4.2), a higher DT than NT (positive DIF) strongly stimulated stem elongation and total stem length was significantly greater than in plants grown with a negative DIF (15/21 °C DT/NT). When plants were illuminated with incandescent lamps, all of them were tall and DIF had no significant effect on stem elongation. Thus, very compact flowering plants were only produced with a negative DIF temperature regimen when day-extension lighting was high in R light. The dry weight of the plants, including the inflorescences, was on average 26% greater with negative DIF compared with positive DIF. Plants grown with a day-extension using incandescent lamps had a higher dry weight than plants grown with fluorescent lamps (Table 3).

TABLE 3

Effects of day/night temperature (DT/NT) fluctuations and different light quality exposures as day-extension lighting with incandescent lamps (INC) or fluorescent lamps (FL) on days to visible bud (VB) and anthesis, total number of flowers and flower buds per plant after a 12 week growth period from the start of continuous lighting (CL), stem length at VB, and anthesis and dry weight at the termination of the experiment of *C. isophylla* 'Blå' plants. DT was applied during the 10 h period with high irradiance (89 μmol s^{-1} m^{-2} PAR) from fluorescent lamps (TL 33). NT was provided during the day-extension period of 14 h by a low irradiance of 0.58 W m^{-2} (400–1000 nm). VB=visible bud. Values followed by different letters are significantly different at the $P<0.05$ level according to Duncan's multiple range test

DT/NT	DIF (°C)	Light source for day-extension	Days to		Total number of flowers and buds	Stem length (cm) at		Dry weight at flowering (g per plant)
			VB	Anthesis		VB	Anthesis	
21/15°C	+6	INC	35 a	68 b	83 a	26.5 a	43.1 a	2.9 b
21/15°C	+6	FL	36 a	71 c	104 b	20.5 b	33.6 b	2.4 a
15/21°C	−6	INC	34 a	65 a	123 d	24.9 a	39.6 a	3.8 c
15/21°C	−6	FL	35 a	67 b	108 c	14.4 c	24.1 c	3.0 b

DISCUSSION

Stem elongation. – Stem elongation in the LDP *C. isophylla* is affected by photoperiod, light quality and day/night temperature alternations (Fig. 2, Table 3, Moe, 1990). Stem elongation is very slow when plants are grown vegetatively at a photoperiod shorter than the critical day length of 14–15 h for flower initiation (Moe and Heide, 1985). Treatments which induce flowering either by day-extension light or by NI increase stem elongation in many LDP, including *C. isophylla* (Fig. 2), *Fuchsia×hybrida* (Vince-Prue, 1977) and *Gypsophila paniculata* (Shillo and Halevy, 1982). Although there is a close relationship between flowering and stem elongation in several LDP, stem elongation and flowering are two independent processes. This independence was also demonstrated by light quality treatments (Fig. 2, Table 1) and DT/NT alternations (Table 3).

It is evident that the rate of internode elongation is a function of the fraction of phytochrome pigment in the FR-absorbing form (Pfr) (Smith, 1986). With long FR or incandescent light (low R/FR ratio of 0.7) treatments during the night, a low Pfr/Ptotal is established and consequently stem elongation in *Campanula* was about 70% greater than in R- or fluorescent light (high R/FR ratio of 4.2)-treated plants, which would have a high phytochrome photoequilibrium (Fig. 2). To produce compact pot plants of *C. isophylla* with good lateral branching, day-extension lighting with R light or fluorescent light with a high R/FR ratio is recommended. The decrease in efficiency to induce elongation with FR light later in the night period (Fig. 2) indicates that the use of incandescent lamps (low R/FR ratio) as NI could be used for induction of flowering in *Campanula.* However, FR lighting inhibited lateral branching (Table 2) and the use of negative DIF to reduce elongation and plant height was nullified when the plants were irradiated with incandescent lamps during the night (Table 3). When the plants were irradiated with fluorescent lamps throughout the night, which established a high Pfr/Ptotal ratio, the plants responded to DIF. A possible hypothesis is that morphological responses induced by DIF, such as internode elongation and lateral branching, are mediated through phytochrome (Moe and Heins, 1990).

Flowering. – *Campanula isophylla* is an obligatory LDP which requires a 14–15 h photoperiod to flower (Moe and Heide, 1985). A 3 h NI just after the middle of a 12 h night (7–9 h) resulted in VB at just as early a stage as with CL, but CL resulted in faster flower development (earlier anthesis) and more flowers per plant than NI. Such a quantitative response of longer photoperiod has been reported for the LDP *Dianthus* (Moe, 1983) and *Gypsophila* (Shillo and Halevy, 1982). The response of flowering to R and FR light seems to change during the night in *Campanula* (Fig. 2, Moe and Holmenlund, 1989). A low Pfr/Ptotal ratio established at the beginning of the night period with

FR lighting promotes flowering, whereas it has an inhibiting effect on flowering 10–12 h later, just prior to the beginning of the day period (Fig. 2). A change in response to light quality during the night period can be attributed to endogenous rhythms in the plants (Bünning, 1977; Heide et al., 1986). Certainly, it has been reported that there is a rhythm of sensitivity to Pfr which inhibits induction of flowering at certain times (Vince-Prue, 1984).

A mixture of R+FR light from incandescent lamps frequently has a much greater effect than R alone in accelerating flowering in many LDP. Therefore, Vince-Prue and Canham (1983) concluded that there seems to be little commercial justification for using fluorescent lamps to control flowering in LDP. However, light sources high in FR light (e.g. incandescent lamps) cause increased stem elongation and inhibition of lateral branching in *C. isophylla* (Table 2) and in a wide range of species grown under SD or LD conditions (Heins and Wilkins, 1979; Moe and Andersen, 1989). Therefore, to obtain compact and good branching plants, a light source high in FR light for either photoperiodic lighting or for supplementary lighting must be avoided. Day-extension with fluorescent lamps or other light sources, such as high-pressure sodium lamps, can effectively induce flowering in *C. isophylla* without causing excessive internode elongation and inhibition of lateral branching.

Changing the daily temperature program from positive DIF (DT>NT) to negative DIF (DT<NT) has a great impact on stem elongation in many plant species (Erwin et al., 1989; Moe and Heins, 1990). DIF has a slight influence on days to anthesis in *Campanula* (Table 3); the overall effect of temperature on flower development is mainly controlled by ADT (Moe, 1990; Moe and Heins, 1990).

The total number of flowers and flower buds, and dry weight of the plants, were greater with negative DIF than with positive DIF. Similar findings were reported by Tangerås (1979) for *Fuchsia* grown under a long photoperiod.

It is concluded from this study that high-quality pot plants of *C. isophylla* can be produced without the use of growth retardant applications when the plants are grown with negative DIF (about −4–6°C), ADT of about 18–20°C and day-extension lighting with fluorescent lamps.

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