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Cost-efficient light control for production of two campanula species

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A B S T R A C T

A cost-efficient light control system based on weather forecasts, electricity prices and daily photosynthesis integral (DPI) was evaluated for application in the commercial production of the long-day (LD) plant Campanula portenschlagiana 'Blue Get Mee' and C. cochlearifolia 'Blue Wonder'. Experiments were conducted under both autumn and spring conditions and included four treatments. Three treatments were controlled by the software system Dynalight Desktop which automatically defined the most cost-efficient use of supplemental light, based on a predefined set point of DPI, forecasted solar irradiance and the market price on electricity. The set points of DPI in the three treatments were 300, 450 and 600 mmol CO2 m−2 leaf d−1 and the treatments were compared with a traditional LD 19-h treatment. The DPI-based light control strategy resulted in very irregular light patterns including daily periods of solar irradiance combined with supplemental light in low light periods and a night period interrupted by irregular light breaks (NB-lighting). Both campanula species flowered in the DPI-based treatments during spring, but the flowering percentage was low and non-uniform during autumn. This was caused by a combination of the irregular light, low natural light intensities and a decrease in daily light integral (DLI), and could be restored by maintaining a continuous 19 h photoperiod with incandescent lamps (<5 μmol m−2 s−1), illustrating that photoperiod was an important factor for flowering in LD species grown under low light intensities. Growth in terms of carbon gain was marginally affected by the irregular light and a 25% reduction in electricity costs was achieved without major reductions in plant quality in spring. Our results illustrate that plant production of LD species can be maintained in a cost-efficient light control system where the use of supplemental light is based on weather forecasts and electricity prices.

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1. Introduction

Protected plant production systems in the northern hemisphere increasingly rely on the addition of supplemental light both to extend the day length and to increase the daily light integral (DLI). However, as electricity prices vary on an hourly basis, the sustainable and optimal use of supplemental light is highly linked to the use and cost of electricity. In a recent developed light control system the timing and use of supplemental light is based on weather forecasts and electricity prices and controlled by predefined set points for daily photosynthesis integral (DPI) (Markvart et al., 2009; Kjaer and Ottosen, 2011). This means that the daily light hours will not occur continuously, but instead divided into periods of solar irradiance combined with supplemental light in low light periods during the day, and a night period interrupted by irregular light breaks (NB-lighting). Furthermore, the length of the NB lighting periods is based on set points for DPI and forecasted solar irradiance. Campanula portenschlagiana 'Blue Get Mee' and C. cochlearifolia 'Blue Wonder' are long-day (LD) plants and recommended greenhouse production conditions for different campanula species include a minimum photoperiod of 14 h (Moe and Heide, 1985). However, rapid and uniform flowering can also be achieved when campanula and various other species of LD plants are illuminated with incandescent light (2–5 μmol m−2 s−1) for 4 h of NB lighting in the middle of a 12 h night (e.g. 2200–0200 h) or continuous light is provided by incandescent lamps during the entire night (Moe et al., 1991; Runkle et al., 1998). If the periods of NB lighting are shorter than 4 h, flowering may become non-uniform and delayed in some species (Runkle et al., 1998), and if the periods are longer than 4 h, the number of flowers may not increase further (Albrecht and Lehmann, 1991; Hamaker et al., 1996). Cyclic lighting, in which lamps are turned on and off during the 4 h of NB lighting in the middle of the night provide advantages in the form of energy savings, but flowering in some LD species may be incomplete, delayed or non-uniform compared to plants grown under continuous incandescent light (Rickford and Dunn, 1972; Blanchard and Runkle, 2010).

Abbreviations: DLD, Daily Light duration; DPI, Daily photosynthesis integral; NB, Night break.

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Our alternative approach is based on controlling the timing and use of supplemental light in relation to hourly changes in electricity prices and forecasted solar irradiance in combination with predefined DPI’s. The advantage of this approach is energy saving in high-cost periods during the day due to reduced use of supplemental light, but the occurrence of shorter day (SD) may delay flowering or provide incomplete and non-uniform flowering due to a highly unpredictable light pattern. Plants have a circadian rhythm based on light-regulated processes (Dodd et al., 2005; Resco et al., 2009). Our hypothesis is that the irregular changes in the distribution and duration of the light periods will disturb the circadian rhythm. However, these disturbances will not affect overall plant dry matter production as recently reported for the SD plant chrysanthemum (Kjaer and Ottosen, 2011). Furthermore, several different strategies of NB lighting have not delayed flowering in campanula (Moe et al., 1991; Runkle et al., 1998; Blanchard and Runkle, 2010), suggesting that the development of induced flowers in this species and other LD plants depend more on the duration of light than on the distribution of light during the day. The aim of the present study was to evaluate whether the occurrence of SD and a highly unpredictable light pattern had any negative effect on growth and development on campanula LD plants.

2. Material and methods

2.1. Plant material and growth conditions

600 plantlets of C. portenschlagiana ‘Blue Get Mee’ and C. cochlearifolia ‘Blue Wonder’ were received from a commercial grower (PKM A/S, Odense, Denmark) in 10.5 cm pots. Plants were fertigated by flooding every second day with nutrient solution consisting of 5.7 mM NaNO₃, 12.6 mM NH₄NO₃, 8.9 mM KCl, 0.7 mM Fe-EDTA, 47.6 mM KNO₃, 0.4 mM (NH₄)₂SO₄, 3.4 mM (NH₄)H₂PO₄, 2.6 mM KH₂PO₄, 5.8 mM MgSO₄ and micronutrients.

The experiment was carried out from 9 October to 18 December 2009 and repeated from 12 January to 26 March 2010 in a greenhouse located at the Department of Horticulture, University of Aarhus (Aarslev, Denmark, Lat 55° N). During this period, the natural day length decreases from 11 h in early October to 7 h in mid December, and increases from 7.5 h to 12.5 h from January to late March. The experiment was performed in two compartments each 9.9 × 7.6 m which were subdivided in two units to allow for a total of four treatments with different light settings. The set point for CO₂ was 700 μl·l⁻¹ during the light periods (day or supplemental light), the night temperature was 15 °C and the average day temperature was 18 °C. Supplemental light provided =60 μmol m⁻² s⁻¹ at table level by high-pressure sodium lamps (SON-T agro, 600 W, Philips, Eindhoven, The Netherlands).

The supplemental light control strategy was the same in all treatments and based on a leaf photosynthesis model that calculated optimum photosynthesis at a given light intensity as a function of leaf temperature and CO₂ concentration (Aaslyng et al., 2003). The set points were adjusted every 10 min based on actual irradiance and temperature, in an attempt to optimize the CO₂ level based on the leaf photosynthesis model, with the overall aim of reaching 80% of the optimum photosynthesis. In the LD treatment, the continuous 19-h light period was maintained from 2200 h to 1700 h by turning on the supplemental light when the photosynthetic photon flux density (PPFD) was below 196 μmol m⁻² s⁻¹. In the three other treatments the timing and use of supplemental light was controlled by 24-h forecasted solar irradiance and hourly changes in electricity prices during the hours from 2000 h to 1700 h by the software package developed in connection with the project (DynaLight Desktop, University of Southern Denmark, Odense, Denmark).

At the beginning of the experiment, a set point for the daily photosynthesis integral (DPI) was defined for each treatment in the DynaLight program. For the three treatments, the DPI’s were 300, 450 and 600 mmol CO₂ m⁻² leaf d⁻¹. Every day at 1900 h, the supplemental light settings for the subsequent 24 h was calculated in three steps for each of the three treatments: (1) The expected DPI was calculated based on the forecasted solar irradiance obtained from the Danish Metrological Institute (DMI, 2011), (2) if the set point for DPI was not reached by solar irradiance, the software calculated the most price-efficient timing of using supplemental light based on the electricity costs obtained from NordPool (Nord Pool Spot, 2011), (3) DynaLight then automatically transferred the resulting set points for timing and use of supplemental light to the climate computer (LCC Completa Semmatic, Sendersø, Denmark) and defined the light periods during the subsequent 24 h. The three treatments were named 300 NB, 450 NB⁺ and 600 NB where NB refers to night breaks of light and the * refers to an additional light setting of continuous lighting with <5 μmol m⁻² s⁻¹ at plant level from 2200 h to 1700 h by four incandescent lamps. An example of how the light periods were distributed in the four treatments during a three day period in autumn is shown in Fig. 1.

**Fig. 1.** An example of daily light duration (LD) and light intensities (μmol m⁻² s⁻¹) of solar irradiation (dark areas) and supplemental light (grey areas) in four greenhouse treatments with different light control strategies. The treatments were long day (LD) with a day length of ~19 h, 600 NB with a set point for daily photosynthesis integral (DPI) of 600 mmol CO₂ m⁻² leaf d⁻¹, 450 NB⁺ (DPI ~450 mmol CO₂ m⁻² leaf d⁻¹) and including ~19 h incandescent light (~5 μmol m⁻² s⁻¹), and 300 NB (DPI ~300 mmol CO₂ m⁻² leaf d⁻¹). NB refers to irregular night breaks of light.
Inside the greenhouse, light intensity (PFD), air temperature, relative humidity (RH) and CO₂ concentrations were recorded in each treatment at table level. Additionally, the state of supplemental light (on or off) was recorded. The PPF was recorded at a weather station above the greenhouse, and the light transmission factor of the greenhouse (0.5) was used to calculate the light intensity inside the greenhouse. The daily light integrals (DLI) from supplemental light and natural PPF were summed. Daily light duration (DLD) was calculated as the number of hours of solar irradiation during the day plus the total number of hours the supplemental light was turned on during the night (length of NB). For the 450 NB⁺ treatment the calculations of DLD were both including and excluding the additional hours of incandescent light (Fig. 2).

2.2. Plant growth and physiology

During the autumn experiment, six plants of each campanula cultivar were harvested prior to the start of the experiment (9 October 2009). Eight plants of each cultivar were harvested both after 24 days (11 November 2009) and at the end of November (9 October 2009). Eight plants of each cultivar were then harvested after 70 days (14 December 2009) and from the Blue Wonder after 47 days (18 December 2009). During the spring experiments the same procedure was followed with a harvest prior to start of experiment (12 January 2010), after 24 days (5 February 2010) and at the end of experiment; ‘Blue Get Mee’ and ‘Blue Wonder’ after 70 days (26 March 2010). The fresh weight (FW) and dry weight (DW) of leaves were recorded at each harvest and the number of flowers was counted at the end of the experimental period.

CO₂ assimilation was measured on three plants of the cultivar ‘Blue Get Mee’ grown in LD on the 18 October 2009, using a portable open infrared gas-exchange system (CIAS-2, PP-systems, Hitchin, United Kingdom). A fully matured leaf was clamped into a leaf cuvette (2.5 cm²) with light, humidity and temperature control. A light response curves was developed within the range of 0–1600 μmol m⁻² s⁻¹. The CO₂ concentration was 600 μl l⁻¹ and the temperature was 18 °C.

2.3. Calculation of electricity costs

The electricity cost to deliver 60 μmol m⁻² at table level by the four high-pressure sodium lamps (SON-T agro) placed in each treatment was estimated to 90 W m⁻². Based on this installation the cost of electricity was calculated in relation to the price on electricity during the exact hours the supplemental light was turned on in the different treatments. The calculations were carried out using a software package (Dynalight Web; University of Southern Denmark, Odense, Denmark). The climate data from the greenhouse climate computer was uploaded to Dynalight Web and calculations of electricity use in kWh m⁻², and price of electricity in euro (€/m²) were based on the climate data and hourly changes in electricity prices obtained from NordPool (Nord Pool Spot, 2011). Calculations of DPI (mmol CO₂ m⁻² leaf) were based on the climate data and the leaf photosynthesis model described by Aasløk et al. (2003).

2.4. Statistical analysis

Statistical analyses were carried out using the R-language ‘stat’ package, release 2.12.0 (R Foundation for Statistical Computing, 2010). Climatic data was extracted from the environmental climate computer and values of means, max, min, sum and standard errors of PPF and hours of light were calculated in relation to treatment using the ‘SummaryBy’ work package (dob)by. The effect of time and treatment on total means of climatic parameters and harvest data of plant DW and number of flowers were analysed by a generalised
linear model allowing for nested random effects (GLM-function). Means of the different treatments were separated by a pairwise t-test using the Holm correction (95% confidence intervals).

3. Results

3.1. Climate

The DLI decreased from 5.1 ± 0.3 to 1.9 ± 0.1 \( \mu \text{mol m}^{-2} \text{d}^{-1} \) during the autumn experiment and increased from 1.5 ± 0.3 to 5.7 ± 0.4 \( \mu \text{mol m}^{-2} \text{d}^{-1} \) during the spring experiment (Fig. 2a and b). This was expected due to the decrease/increase in natural day length and solar irradiance during the two periods and this associated, resulted in a larger contribution of supplemental light to DLI in the autumn experiment in comparison to the spring experiment (Table 1). This also resulted in longer periods of NB lighting during the last five weeks in autumn compared to the same period in spring (Fig. 2d and e).

The 24 h duration of light periods varied between subsequent days in both the 300 NB and 600 NB treatments (results not shown).

Table 1

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Treatment</th>
<th>DLI (( \mu \text{mol m}^{-2} \text{d}^{-1} ))</th>
<th>DLD (h ( \text{d}^{-1} ))</th>
<th>SL (% DLI)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autumn</td>
<td>LD</td>
<td>3.0 ± 0.2 a(^b)</td>
<td>18.4 ± 0.1 a</td>
<td>67.6 ± 3.0 a</td>
</tr>
<tr>
<td></td>
<td>600 NB</td>
<td>2.6 ± 0.2 b</td>
<td>18.4 ± 0.3 a</td>
<td>62.0 ± 3.4 a</td>
</tr>
<tr>
<td></td>
<td>450 NB*</td>
<td>2.1 ± 0.2 b</td>
<td>14.9 ± 0.3 b</td>
<td>54.3 ± 3.6 b</td>
</tr>
<tr>
<td></td>
<td>300 NB</td>
<td>1.7 ± 0.2 c</td>
<td>11.3 ± 0.3 c</td>
<td>41.2 ± 3.9 c</td>
</tr>
<tr>
<td>Spring</td>
<td>LD</td>
<td>4.4 ± 0.3 a</td>
<td>19.3 ± 0.1 a</td>
<td>32.6 ± 2.3 a</td>
</tr>
<tr>
<td></td>
<td>600 NB</td>
<td>4.0 ± 0.2 ab</td>
<td>16.5 ± 0.4 b</td>
<td>25.8 ± 2.5 b</td>
</tr>
<tr>
<td></td>
<td>450 NB*</td>
<td>3.6 ± 0.2 ab</td>
<td>13.3 ± 0.3 c</td>
<td>17.5 ± 2.4 c</td>
</tr>
<tr>
<td></td>
<td>300 NB</td>
<td>3.3 ± 0.2 b</td>
<td>10.3 ± 0.2 d</td>
<td>4.5 ± 1.0 d</td>
</tr>
</tbody>
</table>

\(^a\) Treatments were long day (LD) with a day length of \( \approx 19 \text{h} \), 600 NB with a set point for daily photosynthesis integral (DPI) of 600 \( \mu \text{mol CO}_2 \text{ m}^{-2} \text{ leaf s}^{-1} \), 450 NB (DPI = 450 \( \mu \text{mol CO}_2 \text{ m}^{-2} \text{ leaf s}^{-1} \)) and including \( \approx 19 \text{h} \) incandescent light (\( \leq 5 \mu \text{mol m}^{-2} \text{ s}^{-1} \)), and 300 NB (DPI = 300 \( \mu \text{mol CO}_2 \text{ m}^{-2} \text{ leaf s}^{-1} \)). NB refers to irregular night breaks of light.

\(^b\) Different letters indicate significant difference in probability values between treatments within each experiment (\( P < 0.05 \)).
Fig. 4. The average number of flowers per plant at the final harvest. Campanula plants were grown in four greenhouse treatments with different light control strategies. Treatments were long day (LD) with a day length of ≈19 h (black bars), 600 NB with a set point for daily photosynthesis integral (DPI) of 600 mmol CO₂ m⁻² leaf s⁻¹ (light grey bars), 450 NB* with DPI = 450 mmol CO₂ m⁻² leaf s⁻¹ (dark grey bars) and 300 NB with DPI = 300 mmol CO₂ m⁻² leaf s⁻¹ (white bars). Number of flowers on Campanula cultivar ‘Blue Wonder’ in autumn (A), and in spring (B). Number of flowers on Campanula cultivar ‘Blue Get Mee’ in autumn (C), and spring (D). Values are mean values of six plants (±SE). Different letters indicate significant difference in probability values between treatments (P<0.05).

The average DLD per week was constant in the 300 NB treatment, however the average DLD per week increased during autumn and decreased during spring in the 600 NB treatment and for the periods of supplemental light in the 450 NB* treatment. This illustrated that the solar irradiation was a limiting factor for obtaining the set point of DPI in these two treatments (600 and 450 mmol CO₂ m⁻² leaf d⁻¹) by the end of the autumn experiment and in the beginning of the spring experiment compared to the 300 NB treatment (Fig. 2a and b). For the LD and the 450 NB* treatment (when incandescent light was included) the average DLD was constant throughout the experimental period in both autumn and spring and above 18 h (Fig. 2c and d).

The light intensities were relatively low in both experimental periods resulting in an average DLI of 2.4±0.1 μmol m⁻² d⁻¹ in autumn, and 3.7±0.1 μmol m⁻² d⁻¹ in spring. This induced only minor differences in daily means of CO₂, temperature and RH between the treatments. The average values per day across treatments were 695±2.8 μl l⁻¹ CO₂, 18±0.3°C and 68±0.4% RH in the autumn experiment and 650±5.7 μl l⁻¹ CO₂, 18±1°C and 48±1% RH in the spring experiment.

3.2. Plant growth and flowering

The cultivars showed similar trends in plant DW in response to the different treatments in both experimental periods (Fig. 3), but both cultivars accumulated more dry matter during the 10 week period in spring compared to autumn. Plants grown in 600 NB appeared larger than the plants grown in LD, but there was no significant difference in plant DW between these two treatments. Plants grown in the 300 NB were significantly smaller than

| Table 2 |
| Daily photosynthesis integral (DPI) and cost of electricity for supplemental light in four greenhouse treatments with different light control strategies.\(^a\) |

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Treatment</th>
<th>DPI (mmol CO₂ m⁻² leaf)</th>
<th>Electricity use (kWh/m²)</th>
<th>Cost of electricity (€/m²)</th>
<th>Relative use/cost (% max)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autumn</td>
<td>LD</td>
<td>660</td>
<td>100.5</td>
<td>6.31</td>
<td>100/100</td>
</tr>
<tr>
<td></td>
<td>600 NB</td>
<td>522</td>
<td>71.7</td>
<td>4.37</td>
<td>71/69</td>
</tr>
<tr>
<td></td>
<td>450 NB*</td>
<td>413</td>
<td>47.0</td>
<td>2.75</td>
<td>47/44</td>
</tr>
<tr>
<td></td>
<td>300 NB</td>
<td>264</td>
<td>23.0</td>
<td>1.29</td>
<td>23/21</td>
</tr>
<tr>
<td>Spring</td>
<td>LD</td>
<td>782</td>
<td>44.9</td>
<td>2.64</td>
<td>100/100</td>
</tr>
<tr>
<td></td>
<td>600 NB</td>
<td>662</td>
<td>33.5</td>
<td>1.95</td>
<td>75/74</td>
</tr>
<tr>
<td></td>
<td>450 NB*</td>
<td>519</td>
<td>15.5</td>
<td>0.85</td>
<td>34/32</td>
</tr>
<tr>
<td></td>
<td>300 NB</td>
<td>387</td>
<td>2.9</td>
<td>0.16</td>
<td>7/6</td>
</tr>
</tbody>
</table>

\(^a\) Treatments were long day (LD) with a day length of ≈19 h, 600 NB with a set point for daily photosynthesis integral (DPI) of 600 mmol CO₂ m⁻² leaf s⁻¹, 450 NB* (DPI = 450 mmol CO₂ m⁻² leaf s⁻¹) and including ≈19 h incandescent light (<5 μmol m⁻² s⁻¹), and 300 NB (DPI = 300 mmol CO₂ m⁻² leaf s⁻¹). NB refers to irregular night breaks of light.
plants grown in all other treatments in the autumn, but were similar in size to plants grown in the 450 NB* treatment during spring. The significant decrease in plant DW when grown in 300 NB was due to a significantly lower DLI and shorter DLD in this treatment (Table 1). However, differences in DLI and DLD between treatments could not explain the slight increase in plant DW in 600 NB or the similarities in plant DW between 450 NB* and the three other treatments. However, for the 450 NB* treatment the continuous lighting with incandescent lamps may have decreased respiration, as $5 \mu\text{mol}\text{m}^{-2}\text{s}^{-1}$ was below the light compensation point for net CO$_2$ assimilation in the cultivar ‘Blue Get Mee’ grown under LD conditions (Fig. 5).

Plants grown in the 300 NB treatment during autumn had less than three open flowers per plant at the time of harvest, and over 50% of the plants had no open flowers (Fig. 4a and c). For plants grown in the 600 NB treatment, 100% of the plants of both cultivars flowered, but 50% of ‘Blue Wonder’ had less than three open flowers and 50% of ‘Blue Get Mee’ had less than 30 open flowers. In contrast, flowering was more pronounced in the 450 NB* and in the LD treatment, but the variation in flower number between individual plants was relatively high. The results illustrated that a continuous long light period (LD), whether achieved by supplemental light ($60 \mu\text{mol}\text{m}^{-2}\text{s}^{-1}$) or by incandescent light ($<5 \mu\text{mol}\text{m}^{-2}\text{s}^{-1}$) was important for maintaining the reproductive development of campanula plants grown with decreasing DLI. In contrast, the number of open flowers was relatively high and uniform for plants grown in all four treatments during spring. Furthermore, the number of flowers was not significantly decreased by NB-lighting or shorter days in the 600 NB treatment compared to the 450 NB* treatment. This indicated that campanula plants were less dependent on a continuous long light period when light intensity was higher and DLI was increasing (Fig. 4b and c). The average maximum light intensity measured per day in spring was $411.3 \pm 28.6 \mu\text{mol}\text{m}^{-2}\text{s}^{-1}$ in contrast to $210.8 \pm 20.6 \mu\text{mol}\text{m}^{-2}\text{s}^{-1}$ measured in autumn.

3.3. Electricity costs

The relative savings in electricity costs in the three DynaLight strategies in comparison to the traditional LD treatment were similar in the two experiments (Table 2), but the use of electricity was more than 50% higher in autumn than in spring due to increased use of supplemental light. In spring, 25% savings were achieved on both electricity use and electricity cost in the 600 NB treatment compared to LD. In contrast the DPI was only reduced by 20% in this treatment. When decreasing the electricity use in both autumn and spring, the cost was always further decreased illustrating a beneficial effect of using the supplemental light in low-cost periods.

4. Discussion

It is evident that large savings in electricity costs can be achieved by growing campanula species under supplemental light control strategies based on forecasted solar irradiance and electricity prices regulated by predefined DPI’s. The flowering percentage was uniform in all treatments in spring conditions and differences in the number of flowers per plant were mainly related to differences in DLI as also seen in other plants, for example Salvia splendens, Tagetes patula and Cyclamen persicum (Moccaldi and Runkle, 2007; Oh et al., 2009). That the irregular light conditions only marginally affected the reproductive development of the plants grown in spring was shown in a similar or even higher number of flowers per plant in the 600 NB compared to 450 NB*. Furthermore, the quality of the plants grown in 600 NB was commercially acceptable, and achieved with a 25% reduction in the cost of electricity compared to LD conditions.

The uniform flowering of campanulas in all treatments during spring illustrated that it was possible to maintain flower induction and retain the campanula plants in a reproductive stage during production when the use of supplemental light occurred in a very irregular pattern. However, this was only possible when the DLI was increasing. When DLI was decreasing a high level of variation in the amount of flowers per plant was seen for both species in all treatments in the autumn experiment (Fig. 4). However, LD conditions or conditions where continuous low cost incandescent light was applied during the night triggered the plants to flower, possibly through the effects of the phytochrome system (Moe et al., 1991; Runkle et al., 1998; King et al., 2008; Blanchard and Runkle, 2010). In Arabidopsis LD plants, expression of the FLOWERING LOCUS T (FT) and flowering was promoted by both low-intensity incandescent lamps with a high amount of far-red (FR) light and high intensity red (R) light (King et al., 2008). This illustrated that plants may use both primary controlling factors such as day length and secondary controlling factors such as light intensity and light quality to control flowering in different environments (Bernier and Perilleux, 2005). From the present results, we suggest that the phytochrome response to FR-light played a critical role in flowering of campanula under the low light conditions, whereas the FR-light response and LD conditions were less important under high light intensities and increasing DLI. High light intensities have further been shown to promote long-distance signalling by sucrose supplied through the photosynthetic input, which is crucial for flowering time control in Arabidopsis (Bernier and Perilleux, 2005).

In vegetative chrysanthemums, dry matter accumulation appeared linearly related to the cumulative light integral irrespective of irregular light conditions (Kjaer and Ottosen, 2011). This was not seen in the present study, as plants were similar in size irrespective of differences in DLI between the LD and the 600 NB treatments. This indicated that there was an interaction between the reproductive development of the plants and CO$_2$ assimilation or dry matter allocation to other plant parts when grown under irregular light conditions. Furthermore, differences in leaf anatomy and physiology of the photosynthetic apparatus may have changed the photosynthetic area and light use efficiency of the plants as reported for chrysanthemums grown under irregular light (Kjaer et al., 2011).
and Ottosen, 2011), and for plants grown under LD conditions in comparison to SD conditions (Adams and Langton, 2005).

5. Conclusion

Our results demonstrate that it is possible to grow different species of the LD plant campanula in a climate where the light period is split into a natural light period plus irregular NB lighting. Low natural light intensities during autumn caused non-uniform flowering, and irregular light conditions further impaired the development of flowers. However, this effect was reduced by the use of continuous lighting with incandescent lamps. Under conditions with increasing DLI and higher light intensities, flowering occurred uniformly even though DLD decreased due to a reduced use of supplemental light. These results illustrate that increasing DLI and light intensity are more important for flowering of campanula than the actual day length.

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