TULIP RESPONSE TO DIFFERENT LIGHT SOURCES

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ABSTRACT

Tulip (Tulipa gesneriana L.) is one of the famous potting and valuable cutting flower in floriculture industry as an ornamental plant. Stem elongation, flower quality and flowering time are the important characteristics in tulip flowers. On the other hand, light plays a significant role in the plant growth and flowering in the flowering plants. Therefore, the current study was conducted in a complete randomized design to investigate the effectiveness of using various light colors on the sprouting, morphological, biochemical and flower quality of tulip cv. ‘Princes Catharina-Amalia’. The light treatments included white, blue, red light and dark conditions. The results indicated that days to sprouting and flowering reduced by all light treatments especially at blue light (9.9 and 10.7%, respectively) compared to dark conditions. Moreover, in light treatments, sugar compounds and biomass of tulip plants was better in comparison to dark conditions. According to our results, tulip plants possessed a higher plant yield under blue, red, and white light treatments than dark conditions, especially under blue light. In total, as light can alter morphological, biochemical and the flowering traits of plant, it is suggested to use the changing of light qualities instead of using hormone for various purposes such as cut flowers or pot plants.

Key words: biochemical compounds, flowering, growth responses, light quality, Tulipa gesneriana.

INTRODUCTION

The behavior of plants and animals is often modified by environmental signals such as temperature, watering, light, different stress etc (Gautam et al., 2015; Migdadi et al., 2016). These factors are well known to modify plant morphology (Gautam et al., 2015). Nowadays, a lot of human manipulations are done to alter the morphology of ornamental plants. For example, by using of gamma radiation have changed morphological characters of different cultivars of Lilium (Aslam et al., 2016). Some of these manipulations may be difficult or costly, and some factors may delay or inhibit flowering like temperature manipulations (Langton and Horridge, 2006). Among these environmental signals, light is the foremost factor that can affect plant growth, flowering, photosynthesis, and hormone activity (Pashkovskiy et al., 2016). Light stimulus may boost the endogenous hormonal production and crosstalk of endo and exogenous hormones (Usman et al., 2014). Light is absorbed by plant photoreceptors including phytochromes, cryptochromes and phototropins (Muneer et al., 2014). Thus, plants can detect and respond to changes in light intensity, duration and spectrum (Hayes et al., 2014). Light quality (spectrum or wavelength) is also important for the light response in plants (Sumtomo et al., 2012). Therefore, change in the spectrum light is beneficial for plant growth and flowering (Li and Kubota, 2009). Considering the fact that using of artificial light is widely common in greenhouse productions. There is strong need for alternative strategies to control plant growth and manipulation of light is an important topic in greenhouse productions. Artificial lighting systems have recently been presented as a potential technology for making systems more sustainable and improving plant growth (Darko et al., 2014). Tulip (Tulipa gesneriana L.) is a perennial bulb flower and a popular ornamental bulbous plant, which belongs to the Liliaceae family. With a history of more than 400 years, the tulip has become one of the world’s most important ornamental plants. It is one of the commercially important bulbous ornamental plants owing to its unsurpassed beauty and economic value (Jhon and Neelofer, 2006). In this case, most studies have been covered effect of chemical treatment on tulip forcing, growth and flowering, but little research has been done about effect of light on tulip. Red and blue lights have the greatest influence on the growth of plants because they are the main source of energy for photosynthesis (Lin et al., 2013), and each of them have special effects on plant response. For instance, in one experiment, the earliest opening and coloring in inflorescence buds observed when chrysanthemum plants were placed under blue light. Moreover, under white and blue light the highest number of developed flower heads was found (Jerzy et al., 2011). It has been reported that the red light decreased the thickness of the abaxial face and spongy tissues, while the blue light increased the thickness of the
epidermis and palisade mesophyll cells (Macedo et al., 2011). Massa et al. (2008) found that photosynthesis rate in plants grown under combination of red and blue light more than red lights only. It is presumed that different light quality can provide a range of benefits to the flowering, growth and some biochemical traits of tulips. Therefore, to the best of our knowledge, there is no comprehensive study about different light sources on tulip sprouting and growth. Hence, the objective of the present study was to evaluate the flowering behavior of tulip plants under various artificial color lights.

**MATERIALS AND METHODS**

The present experiment was carried out at Department of Horticulture, Science and Research Branch, Islamic Azad University, Tehran (Iran). Healthy and uniform bulbs of tulip cv. ‘Prinses Catharina-Amalia’ with circumferences 12 cm were supplied by Mahde Laleha, Institute of Gachsar (Iran). Bulbs were cooled at 4 °C for 10 weeks (before application of treatments) and to prevent from fungal diseases, the tulip bulbs were disinfected with Benomyl fungicide 3 g L⁻¹ for 25 min and were exposed to air 70 min. Then, the bulbs were placed in 10 cm plastic pots contain 70% peat and 30% perlite, and covered by sandy soil. Pots were kept in phytotron chambers under different light conditions. The average temperature during experiment was in the range of 15-17 °C and the average daily relative air humidity (RH) was 60-70%. Irrigation (without fertilization) was also done every three days. The number of repetitions was 3 replications. Each replication was consisted of 6 experimental units. After that, the light treatments were applied until the end of experiment. The light treatments were white, blue, red, and dark conditions. Plants were placed in laboratory under three fluorescent lamps for each color (Philips TLD) with 36 W power at 60 cm above soil level; white color (370-700 nm), blue color (400-580 nm), red color (600-700 nm) for 16/8 h light/dark conditions, and dark treatment (without any light application during experiment). It is worth mentioning that artificial lights were the only means of light supply, and they were well isolated to prevent potential contamination with other light sources. Data recording was begun with start of sprouting. Days to sprouting of bulbs (day), days to flowering (day), percentage of sprouting and flowering plants (%) were recorded during the experiment. Plant height (cm), length of upper and lowest internodes (cm), length and width of the lowest leaf (cm), and number of leaves per plant, flower diameter at the time of flower opening, length of flower bud were determined when the flower buds were fully colored. Leaf area was assayed by a portable leaf-area meter (Model AM200, ADC Bio-Scientific Ltd.). The leaf greenness index (SPAD) was also measured using a chlorophyll meter (SPAD-502). In order to do so, the leaves from the outer whorl of each plant were measured three times and the means were calculated at the stage of flowering.

Total sugar were determined according to Sadasivam and Manickam (1992) and fructose, sucrose, and glucose were determined according to (Ashwell, 1957) in bulbs during bulb sprouting. The activity of α-Amylase was estimated using the method of Chong (1979). Anthocyanin contents was quantified by measuring the amount of anthocyanins in fresh ray florets as described by Meng and Wang (2004) when the flowers were fully colored.

Data were analyzed by one-way analysis of variance using the SAS software (Version 9.1, SAS Institute Inc., Cary, NC, USA). The difference among treatment means was statistically compared using Duncan’s multiple range test ($P \leq 0.05$). Correlation was also observed between traits using the SPSS version 17 (SPSS Inc., Chicago, IL, USA).

**RESULTS AND DISCUSSION**

The results, presented in Table 1, showed that days to sprouting significantly declined under blue light conditions. Days to flowering also reduced by light treatments application compared to dark conditions. Sprouting and flowering percentage increased as a result of all light application relative to dark conditions. However, bulb sprouted even in dark conditions, while flowering affected by light treatments. Moreover, length of first and last internode increased at dark and blue light conditions, respectively. A similar trend observed for plant height. Surprisingly, the highest flower diameter observed at red light conditions. Consequently, all of light treatments (white, blue, and red) caused an increasing in length of flower in comparison with dark conditions (Table 1).

In our study, flowering percentage significantly increased at blue and white light conditions. Previous studies showed that blue light promoted flowering compared with control and red light conditions (Gautam et al., 2015). Flowering in strawberry plants was also earlier in plants grown under blue light than red light (Yoshida et al., 2012). In contrast with our results, Sumitomo et al. (2012) reported that the number of days to flowering not affected by light treatments. They noticed that the trend was the same for all light conditions in tulip cultivars including ‘Leen van der mark’, ‘Murasaki suisho’ and ‘Kikomachi’. The effects of light to flowering time and plant growth are species specific (Singh et al., 2015). The results of the present study are consistent with those of Šmigelska and Jerzy (2011), who reported that Hyacinthus orientalis L. Forced in blue and red lights to flower.

In the present study, plant height increased under blue and dark conditions. Maybe the reason of this...
phenomenon can explain by increasing first and last internode under dark and light conditions, respectively. In line with our results, dark conditions leads to an increase in length of the first internode, whereas the last internode was the longest one when grown under natural light conditions (Okubo and Uemoto, 1985). The results of Smigielńska et al. (2014) showed that blue light forced the length of first internode in tulip, while red light stimulated last internode elongation. Stem elongations in response to changes in light quality may be mediated by changes in GA level (Campell and Bonner, 1986) or sensitivity to GA (Ross et al., 1990).

A similar trend was observed by Gautam et al. (2015), who found that blue light led to significant increases in the stem elongation and plant height and caused a more upright shoot orientation. Jeong et al. (2014) reported a similar trend, indicating that stem length of chrysanthemum were increased at 15 h of mixed red and blue light and then 4 h of supplemental blue light. For instance, an increase in stem elongation of some bedding flowers were observed by application of red light (in Impatiens balsamina), and blue light (in Petunia × hybrida) (Akbarian et al., 2016). In other studies, it has been shown that blue light suppresses stem elongation in roses and poinsettia (Islam et al., 2012; Terfa et al., 2013). Thus, the effect of blue light on stem elongation is proposed to be affected by intensity, duration, and spectrum light. There is also evidence that internodes elongation is controlled by a blue light receptor and by phytochromes (Smith, 1994). Increasing plant height using blue light explained by Kigel and Cosgrove (1991), who stated that red light can inhibit the availability or sensitivity of auxin. They also observed an opposite trend for blue light. However, both blue and red light are considered to enhance the photosynthesis efficiency and chlorophyll value that lead to an increasing in plant growth and production (McCree, 1972). In addition, in this study, the value of the leaf greenness index (SPAD) increased at all light conditions and in blue light was more than other light conditions. There was a positive and significant correlation (Table 4) between leaf greenness index (SPAD) and plant height of tulips \( r = 0.78, P \leq 0.01 \).

Fresh weight of plants increased as a result of blue and red colors, respectively, relative to dark and white colors. The fresh weight of bulb, dry weight of shoot and bulb significantly increased at all light conditions compared to dark conditions. The highest leaf width and leaf area recorded at red light conditions in comparisons with other treatments (Table 2). In our study, the highest leaf greenness index was observed at blue light in comparison with other light conditions. Smigielńska and Jerzy (2011) observed that yellow light increased the leaf greenness index of hyacinth cv. ‘Anna Marie’, ‘White Pearl’ and ‘Blue Star’. A significant and positive correlation (Table 4) was also observed between leaf area and leaf greenness index \( r = 0.79, P \leq 0.01 \).

The results of Muneer et al. (2014) showed that the highest biomass and elongation of lettuce was observed at blue light than red and green light. Similarly, Shimokawa et al. (2014) founded that blue and red light promoted plant growth. However, they reported that leaf length and width of lettuce increased in plant when grown under red light conditions than at blue and fluorescent light ones. Additionally, in present research, it seems that plant height can increase in blue light and dark conditions, while fresh and dry weight increased in blue light conditions but not in dark conditions. Photosynthesis is the base of plants growth, synthesizing almost 95% dry weight for plant. Thus, in dark conditions because of lack of photosynthesis lights leads to a decrease in dry matter (Wang et al., 2013).

The results indicated that the parameters such as total sugar, glucose, sucrose, and fructose dramatically affected by all light conditions (blue, red, and white) compared with dark conditions (Table 3). Therefore, \( \alpha \)-Amylase significantly increased with light treatments. Similarly, the leaf greenness index (SPAD) also increased at all light conditions, relative to dark conditions. Scale of blub contains a lot of carbohydrate, fructose, sucrose, and glucose (Ohyama et al., 2006). These results are contrary to the reports of Bergmann and Bälz (1966), who founded that there was no difference between blue and red light on carbohydrate content of tobacco tissue, while Samuoliene et al. (2010) reported an increased in the amount of carbohydrate accumulation in strawberry plants grown under red and blue lights. All light conditions increased total sugar, \( \alpha \)-Amylase, and other sugar compounds such as fructose, glucose, and sucrose. This trend may cause an increasing in plant height, shoot and bulb fresh and dry weight. In contrast with our results, Chidburee et al. (2008) reported that the highest total sugar, sucrose, fructose, and glucose were obtained when the plants were grown under natural light than red light. This inconsistency may have occurred due to the differences between plants, light and conditions. In this regards, correlation analysis showed a positive and significant correlation (Table 4) between plant height with \( \alpha \)-Amylase \( r = 0.95, P \leq 0.01 \), and sucrose \( r = 0.97, P \leq 0.01 \). Hence, it can be postulated that light treatments (especially blue light) increased plant height of tulip through increasing sucrose and total sugar in bulbs because the source of sucrose in bulbs is effective for elongation. Our findings are in agreement with Sato and Okubo (2006), who stated that by increasing \( \alpha \)-Amylase, the starch converted to sugars which lead to a higher plant.

The highest leaf greenness index (SPAD) and anthocyanin content was detected under blue lights (Table 3). In fact, biosynthesis of anthocyanins as response phytochemical in this plant, showed more
sensitive to blue light. Accumulation of anthocyanins in plants can be affected by external environmental factors, among which light is the most important one (Grisebach, 1982). Dependence anthocyanin biosynthesis to light significantly depends on the species and the experimental conditions (Mancinelli et al., 1991). For example, production of anthocyanin by strawberry cells depends on both of light intensity and the light/dark cycle operation (Kurata et al., 2000). Mizuno et al. (2011) reported that anthocyanin content in Brassica olearacea plants increased by lighting with 640 nm red LEDs. Similar ly, Sing et al. (2015) concluded that red and blue light enhanced carotenoids, vitamin C, anthocyanins, and polyphenols. According to results of Gude and Dijkema (1992), anthocyanin increased in the purple colored cultivars of hyacinths using blue lights in comparison with red lights. However, flower diameter increased under red light compared with dark conditions. Moreover, our results showed that there was a significant and positive correlation (Table 4) between flower diameter with total sugar (r = 0.85, P ≤ 0.01) and fresh and dry weight of bulbs (r = 0.76, P ≤ 0.01). Therefore, it seems that the fresh weight of bulbs and total sugar have affected the flower diameter of tulips.

Table 1. Effect of different light treatments on some morphological and flowering traits of tulip.

<table>
<thead>
<tr>
<th>Light treatments</th>
<th>DS (day)</th>
<th>DF (day)</th>
<th>Sprt (%)</th>
<th>flw (%)</th>
<th>PH (cm)</th>
<th>LFI (cm)</th>
<th>LLI (cm)</th>
<th>LN (no.)</th>
<th>LFB (cm)</th>
<th>FD (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>W</td>
<td>19.77a</td>
<td>38.70b</td>
<td>100a</td>
<td>83.33a</td>
<td>32.16b</td>
<td>8.83bc</td>
<td>8.16c</td>
<td>3.00a</td>
<td>4.86a</td>
<td>3.83b</td>
</tr>
<tr>
<td>B</td>
<td>18.22b</td>
<td>38.80b</td>
<td>100a</td>
<td>83.33a</td>
<td>39.50a</td>
<td>11.33ab</td>
<td>14.25a</td>
<td>3.00a</td>
<td>4.66a</td>
<td>3.73bc</td>
</tr>
<tr>
<td>R</td>
<td>20.00a</td>
<td>40.33b</td>
<td>100a</td>
<td>75.00b</td>
<td>33.00b</td>
<td>6.66c</td>
<td>8.50c</td>
<td>3.00a</td>
<td>4.30a</td>
<td>5.40a</td>
</tr>
<tr>
<td>D</td>
<td>20.23a</td>
<td>43.42a</td>
<td>94.4b</td>
<td>38.88c</td>
<td>42.16a</td>
<td>14.66a</td>
<td>10.33b</td>
<td>3.00a</td>
<td>3.23b</td>
<td>2.83c</td>
</tr>
</tbody>
</table>

The mean values with different letters across treatments are significantly different at P ≤ 0.05.

Abbreviations: W, White; B, Blue; R, Red; D, Dark; DS, Days to sprouting; DF, Days to flowering; Sprt, percentage of sprouting; flw, percentage of flowering; PH, Plant height; LFI, Length of first internode; LLI, Length of last internode; LN, Leaf number; LFB, Length of flower bud; FD, Flower diameter.

Table 2. Effect of different light treatments on fresh and dry weight (plant and bulb), and leaf characteristics of tulip.

<table>
<thead>
<tr>
<th>Light treatments</th>
<th>FW shoot (g)</th>
<th>DW shoot (g)</th>
<th>FW bulb (g)</th>
<th>DW bulb (g)</th>
<th>Leaf area (cm²)</th>
<th>Leaf length (cm)</th>
<th>Leaf width (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>W</td>
<td>8.75b</td>
<td>1.31a</td>
<td>21.69a</td>
<td>6.29a</td>
<td>58.81ab</td>
<td>19.5ab</td>
<td>4.06b</td>
</tr>
<tr>
<td>B</td>
<td>9.89a</td>
<td>1.10a</td>
<td>21.54a</td>
<td>6.27a</td>
<td>55.27ab</td>
<td>20.26a</td>
<td>4.5b</td>
</tr>
<tr>
<td>R</td>
<td>9.44ab</td>
<td>1.30a</td>
<td>21.47a</td>
<td>6.24a</td>
<td>68.81a</td>
<td>16.93b</td>
<td>6.73a</td>
</tr>
<tr>
<td>D</td>
<td>7.04b</td>
<td>0.76b</td>
<td>19.37b</td>
<td>5.29b</td>
<td>45.96b</td>
<td>22.00a</td>
<td>3.83b</td>
</tr>
</tbody>
</table>

The mean values with different letters across treatments are significantly different at P ≤ 0.05.

Abbreviations: W, White; B, Blue; R, Red; D, Dark; FW, Fresh weight; DW, Dry weight.

Table 3. Effect of different light treatments on some biochemical traits of tulip.

<table>
<thead>
<tr>
<th>Light treatments</th>
<th>TS (mg/g FW)</th>
<th>Glucose (mg/g FW)</th>
<th>Sucrose (mg/g FW)</th>
<th>Fructose (mg/g FW)</th>
<th>α-Amylase (mg/min/g FW)</th>
<th>ACN (Δ A g-1 FW)</th>
<th>LGI (SPAD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>W</td>
<td>45.14b</td>
<td>8.52a</td>
<td>13.59b</td>
<td>11.05a</td>
<td>25.38a</td>
<td>0.44ab</td>
<td>34.41b</td>
</tr>
<tr>
<td>B</td>
<td>48.34a</td>
<td>8.79a</td>
<td>15.79a</td>
<td>11.09a</td>
<td>27.99a</td>
<td>0.54a</td>
<td>40.73a</td>
</tr>
<tr>
<td>R</td>
<td>44.93b</td>
<td>8.50a</td>
<td>13.67b</td>
<td>11.54a</td>
<td>25.62a</td>
<td>0.41ab</td>
<td>34.63b</td>
</tr>
<tr>
<td>D</td>
<td>39.85c</td>
<td>7.95b</td>
<td>8.44c</td>
<td>9.30b</td>
<td>18.44b</td>
<td>0.31b</td>
<td>8.47c</td>
</tr>
</tbody>
</table>

The mean values with different letters across treatments are significantly different at P ≤ 0.05.

Abbreviations: W, White; B, Blue; R, Red; D, Dark; TS, Total sugar; ACN, Anthocyanin; LGI, leaf greenness index.
Table 4. Correlation coefficients among studied growth indices of tulip plants grown under different light quality.

<table>
<thead>
<tr>
<th></th>
<th>PH</th>
<th>FD</th>
<th>bulb</th>
<th>FW</th>
<th>DW</th>
<th>Leaf</th>
<th>TS</th>
<th>Glucose</th>
<th>Sucrose</th>
<th>Fructose</th>
<th>Amylas</th>
<th>α-Amylase</th>
<th>ACN</th>
<th>LGI</th>
</tr>
</thead>
<tbody>
<tr>
<td>PH</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FD</td>
<td>0.936*</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FW bulb</td>
<td>0.757**</td>
<td>0.765**</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DW bulb</td>
<td>0.764**</td>
<td>0.760**</td>
<td>0.998*</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf area</td>
<td>0.843**</td>
<td>0.941**</td>
<td>0.763*</td>
<td>0.773*</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>TS</td>
<td>0.721**</td>
<td>0.854**</td>
<td>0.977*</td>
<td>0.899*</td>
<td>0.765**</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Glucose</td>
<td>0.440(N)</td>
<td>0.486(N)</td>
<td>0.919*</td>
<td>0.928*</td>
<td>0.566(N)</td>
<td>0.939*</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sucrose</td>
<td>0.975**</td>
<td>0.707*</td>
<td>0.995*</td>
<td>0.938*</td>
<td>0.802**</td>
<td>0.978*</td>
<td>0.924*</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fructose</td>
<td>0.774**</td>
<td>0.839**</td>
<td>0.956*</td>
<td>0.964*</td>
<td>0.903**</td>
<td>0.963*</td>
<td>0.861*</td>
<td>0.962*</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>α-Amylase</td>
<td>0.959**</td>
<td>0.571(N)</td>
<td>0.948*</td>
<td>0.957*</td>
<td>0.650**</td>
<td>0.965*</td>
<td>0.984*</td>
<td>0.956*</td>
<td>0.910*</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anthocyanin</td>
<td>0.428(N)</td>
<td>0.563(N)</td>
<td>0.807*</td>
<td>0.817*</td>
<td>0.343(N)</td>
<td>0.831*</td>
<td>0.967*</td>
<td>0.804*</td>
<td>0.706*</td>
<td>0.935*</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LGI</td>
<td>0.780**</td>
<td>0.607*</td>
<td>0.971*</td>
<td>0.978*</td>
<td>0.793**</td>
<td>0.984*</td>
<td>0.983*</td>
<td>0.977*</td>
<td>0.935*</td>
<td>0.966*</td>
<td>0.908*</td>
<td>1</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**, *, NS; significant at 0.01 level, at 0.05 level and not significant, respectively. Abbreviations: PH, Plant height; FD, Flower diameter; FW, Fresh weight; DW, Dry weight; TS, Total sugar; LGI, leaf greenness index.

Conclusions: The present study revealed that the application of different light sources on tulip leads to a higher plant yield and bulbs quality. Application of different light qualities resulted in an improvement in the growth parameters as well as the biochemical, morphological and the flowering characteristics of tulip. Also showed that flowering date and quality of forced tulips depend on light color. Hence, it is recommended that the color lighting method must be optimized for use under commercial production conditions.

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