

The effect of light quality on the growth characteristics and photosynthetic performance of the *Dracocephalum moldavica* plant

Hossein Nastari Nasrabadi

nastari@t.jamcaas.ac.ir

University of Torbat-e Jam, Torbat-e Jam

Mahboubeh Zamanipour

Velayat University

Mahdi Moradi

University of Torbat-e Jam, Torbat-e Jam

Article

Keywords: Essential oil, photosynthesis, light quality, *D. moldavica*

Posted Date: October 30th, 2025

DOI: <https://doi.org/10.21203/rs.3.rs-7610660/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Additional Declarations: No competing interests reported.

Version of Record: A version of this preprint was published at Scientific Reports on February 3rd, 2026.
See the published version at <https://doi.org/10.1038/s41598-026-37845-9>.

The effect of light quality on the growth characteristics and photosynthetic performance of the *Dracocephalum moldavica* plant

Hossein Nastari Nasrabadi ^{1*}, Mahboubeh Zamanipour ² and Mahdi Moradi ¹

1- Department of Horticulture Science and Engineering, University of Torbat-e Jam, Torbat-e Jam, Khorasan Razavi, Iran

2- Department of Agriculture, Technical and Engineering Faculty, Velayat University, Iranshahr, Iran

*Corresponding author: nastari@tjamcaas.ac.ir

Abstract

Various aspects of light, including intensity, quality, and the period of light irradiation, affect plant growth and development, as well as their response to gas relations. In this study, the effect of different light spectra on growth characteristics, photosynthetic performance, and phenolic content of the *D. moldavica* plant were investigated. To this end, six light treatments including white light (w), red light (R), blue light (B) and three combined lights (R70B30, R50B50, and R30B70) emitted from LED lamps were used in a completely randomized design with three replications. The results revealed a significant effect of different light spectra on the studied traits at the 5% and 1% levels. The combined light of R70B30 improved plant growth characteristics. The height of plants grown in the red light treatment was the highest compared to other treatments. The highest fresh and dry weights of the shoot were observed in the R70B30 light spectrum, and the lowest in the blue light spectrum. Growth indices decreased with increasing proportions of blue light and improved with increasing proportions of red light. The maximum content of photosynthetic pigments was recorded in the combination of red and blue lights. The highest fluorescence intensity in all stages of the OJIP test was observed with red light, and the lowest fluorescence value was recorded with the combined lights of R50B50 and R70B30. The efficiency of the photosystem II water splitting system (F_v/F_0) and the maximum efficiency of the photosystem (F_v/F_m) were minimal in the red light treatment. Red light lowered the efficiency index of the system per absorbed light (PI_{ABS}) and increased the quantum yield of energy loss (ΦD_0), the light absorption rate per reaction center (ABS/RC), and the electron capture rate (TR_0/RC). The highest total phenolic content and antioxidant capacity were observed in plants

grown under the R70B30 light conditions. The highest essential oil content (2.07% vol/wt) was observed in the R70B30 light environment, showing a 113.4% increase compared to white light.

Keywords: Essential oil, photosynthesis, light quality, *D. moldavica*

Introduction

Light is one of the main factors regulating plant growth and development, as well as an energy source for photosynthesis and an important signal that plays a major role in plant growth, morphological characteristics, photomorphogenesis, production of secondary metabolites, cell molecular biosynthesis and gene expression during plant growth ([Aliniaieifard et al., 2018](#); [Huber et al., 2021](#)). Internal signals generated after light exposure can regulate the biosynthesis and growth of carotenoid plastids ([Klem et al., 2019](#)). LED lamps with specific wavelengths of light spectra cause diversity in plant responses. Photosynthetic pigments absorb most red and blue wavelengths, so these lights are more effective for exciting electrons in this photosystem. The effects of red and blue lights on the growth and physiology of various plant species have been studied ([Amiri et al., 2018](#); [Aalifar et al., 2020](#); [Ghorbanzadeh et al., 2020](#); [Seif et al., 2021](#)). Many light sources such as fluorescent lamps, metal halide lamps, high-pressure sodium lamps and incandescent lamps are commonly used in greenhouses to increase the photosynthetic photon flux density for plant growth, but these light sources have some problems, for example, they have low energy efficiency and in some cases, part of their spectrum is not in the range of photosynthetic active radiation and are not suitable for inducing plant growth ([Kim et al., 2019](#)). [Naznin et al. \(2019\)](#) concluded that increasing the blue light ratio is necessary to enhance growth, pigment production, and antioxidant content of plants, although the optimal ratio depends on the species. The effect of light quality and intensity on plants and easy access to different light spectra are an opportunity to use this knowledge to evaluate different light spectra and introduce the best light regime for plants according to market needs. Studies on different plant species have shown that the same light composition has different effects on photosynthetic, morphological and biochemical parameters in different plant species ([Zotov et al., 2020](#)). Therefore, more extensive studies on species and their specific responses to different light spectrum compositions are needed. Plants of the Lamiaceae family are of particular importance due to their essential oil active ingredient. *Dracocephalum moldavica* belongs to the family Lamiaceae, which is used for its antioxidant, antimicrobial, anti-inflammatory, and aromatic

essential oils such as borneol, geranial and geraniol (Amin et al., 2020; Aćimović et al., 2019, Acimovic et al., 2022). Due to its popularity and economic potential, the extensive cultivation of *D. moldavica* has increased in Iran, and more than 300 hectares are dedicated to its growth in West Azerbaijan province alone. In recent years, the cultivation of this plant in greenhouses and controlled environments has been the focus of many studies. Since the light conditions in these places can be adjusted and controlled, investigating the effect of different light spectra on the growth and physiological characteristics of *D. moldavica* can be very informative for choosing the appropriate conditions for cultivating this plant. Therefore, in this study, the effect of different LED light spectra on the growth, photosynthetic, and biochemical characteristics of *D. moldavica* in a controlled environment was studied to introduce the optimal lighting mode for this plant.

Materials and Methods

Plant materials and growth conditions

In order to study the effects of light on the morphological and photosynthetic characteristics of *D. moldavica*, a pot experiment was conducted in a completely randomized design with 6 treatments and 3 replications in the plant growth chamber of the Research Laboratory of the Horticultural Science and Engineering Department of Torbat-e-Jam university in 2024 as soilless cultivation. The seeds of *Dracocephalum moldavica* plant were obtained from commercial company (Pakan Seed company Isfahan). To prepare seedlings, one seed was sown in each hole of the seedling tray. Day and night temperatures were set at 25 and 20 degrees Celsius, respectively. Although the relative humidity in the growth chamber could not be adjusted, its level varied between 40 and 55 percent. Watering was done daily until the seedlings emerged and after the seedlings emerged, feeding was done daily with half Hoagland nutrient solution. After the seedlings reached the 4-leaf stage, seedlings that were vegetatively stronger and almost the same size were selected and transferred to the main pots with a height of 20 and a diameter of 14 cm. After transfer, the plants were grown under different light spectra until the end of the experiment. The cultivation medium of the main pots was a mixture of perlite (40%), cocopeat (40%) and vermiculite (20%). After the main plants were transferred to the pot, feeding was done using Hoagland nutrient solution every other day.

Light treatments

Different light treatments used in this study were contains of white light (W), red (R), blue (B), red: blue (RB) with ratios of (70:30, 50:50 and 30:70). The light intensity was set at 250 ± 10 micromoles photons per square meter per second (PPFD) and with 14 and 10 hours of light and darkness respectively. To apply the light treatments, chambers with dimensions of 2 meters in length, 1.5 meters in width and one meter in height were constructed and equipped with 24-watt LED floodlights with different light spectra. In order to prevent the entry of light from other treatments and also to ensure uniform light dispersion inside the chambers, light insulating fabrics (reflectors) were used around the chambers. The intensity of the photosynthetic photon flux density and the light spectrum were measured using a photometer (Sekonic C-700, Japan) at a distance of 25 cm from the plant surface. The wavelengths of different light spectra are shown in Fig. 1. Following the plant growth, the metal clamps were adjusted to evenly distribute light over the plant surface evenly, maintaining a distance of approximately 25 cm between the lamps and the plant.

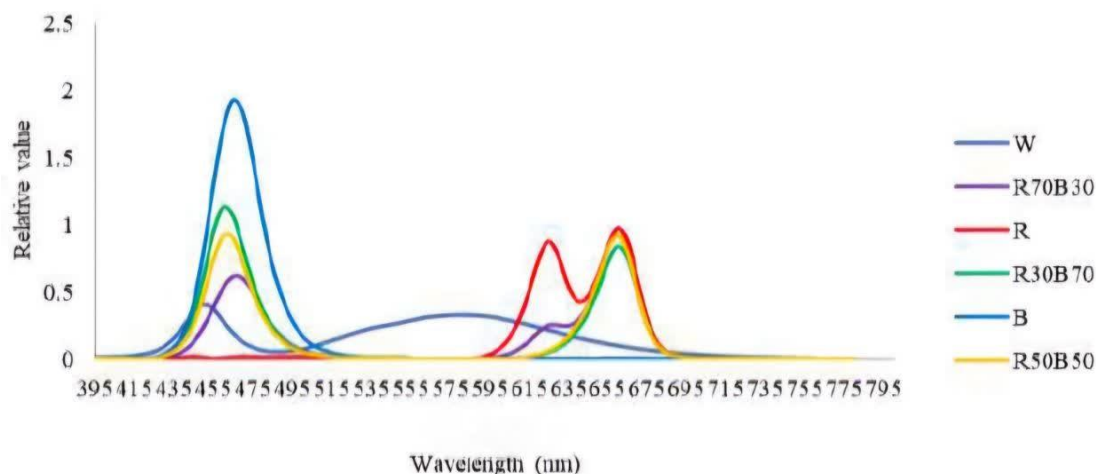


Fig. 1. Light spectra in blue (B), red (R), R50: B50, R70: B30, R30: B70, and white (W) treatments

Measurement of morphological and growth indices

Plant height was measured using a ruler. A leaf area meter (CI-202 Area Meter) was also used to measure the leaf area of each plant (Zuk-Gólaszewska et al., 2003).

Measurement of photosynthetic pigments

The absorbance of the solution at wavelengths of 663 and 646 nm was measured using a spectrophotometer (UV-Vis array, Photonix-Ar2017, Iran). In addition, the amount of photosynthetic pigments was calculated based on milligrams per gram of fresh weight using the following equations (Lichtenthaler and Wellburn, 1983).

$$\text{Chl a (mg/g)} = (12.21 \times A_{663}) - (2.81 \times A_{646})$$

$$\text{Chlb (mg/g)} = (20.13 \times A_{646}) - (5.03 \times A_{663})$$

$$\text{Chl a+b (mg/g)} = \text{Chla} + \text{Chlb}$$

Induction of chlorophyll a fluorescence using the OJIP test

To perform this test, young and developed leaves of plants were first placed in the dark for 20 minutes. Then, by implementing the OJIP protocol, fate of the excited electrons in photosystem II were evaluated (Strasser et al., 2000). Final calculations were performed using PAR-Flourpen software. The measured parameters (Table 1) were analyzed, and the physiology of photosystem and the possible energy flow between the individual parts of photosystem II were studied.

Table 1- The O-J-I-P parameters measured in this study

Abbreviation	definitions	Formula
Basic parameters		
F_0	(O-step of O-J-I-P transient)	F_{50ms}
F_J	Fluorescence rate at the J-step of O-J-I-P	F_{2ms}
F_I	Fluorescence rate at the I-step of O-J-I-P	F_{30ms}
Fluorescence Parameters		
F_m	Maximum fluorescence, when all PSII RCs are closed (P-step of OJIP transient)	$F_{I_s} = F_p$
F_v	Variable fluorescence of the dark-adapted leaf	$F_m - F_0$
ΦP_0	Maximum yield of PSII	$1 - (F_0/F_m)$
Quantum Yields and Efficiencies/Probabilities		
Ψ_0	Electron that moves further than QA^-	ET_0/TR_0
ΦE_0	The quantum yield of electron transport	ET_0/ABS
ΦD_0	Quantum yield of energy dissipation	F_0/F_m
ΦP_{av}	Average quantum yield	$\phi_{P0} (S_M/t_{FM})$
PI_{ABS}	Performance index for the photochemical activity	$[(\gamma RC/1 - \gamma RC) (\phi_{P0} / 1 - \phi_{P0}) (\Psi_{E0} / 1 - \Psi_{E0})]$
Specific Energy Fluxes (Per QA Reducing PSII RC)		
ABS/RC	The energy fluxes per RC	$M_0 (1/V_J)(1/\phi_{P0})$
TR_0/RC	Trapped energy flux (leading to QA reduction) per RC	$M_0 (1/V_J)$
ET_0/RC	Electron transport flux	$M_0 (1/V_J)(1 - V_J)$
DI_0/RC	Dissipated energy flux	$(ABS/RC) - (TR_0 /RC)$

Total phenol measurement

For this purpose, one gram of fresh mature and developed leaf tissue was mixed with 10 ml of 80% methanol and placed on an incubator shaker for 24 hours and were centrifuged at 13,000 rpm for 20 minutes. Total phenol was evaluated using the Folin-Ciocalteu reagent and the method of [Chen et al. \(2013\)](#). For this purpose, 250 μ l of the extract was mixed with 1.75 ml of distilled water and 100 μ l of Folin-Ciocalteu, and after two minutes, one ml of 20% sodium carbonate (Na_2CO_3) was added to it. Then, the samples were kept at room temperature and in the

dark for 2 hours, and their absorption was subsequently measured at a wavelength of 730 nm using a UV-Vis array spectrophotometer (Photonix-Ar2017, Iran).

The amount of phenolic compounds was expressed as micrograms of gallic acid equivalent per gram of fresh weight. Concentrations of 0, 100, 200, 300, 400, and 500 micrograms per milliliter of gallic acid were used to draw the standard curve ([Chen et al., 2013](#)).

Measurement of antioxidant capacity

For measuring of antioxidant capacity, 200 microliters of the prepared extract were synthesized with 1 ml of 0.1 mM DPPH solution and 1.8 ml of distilled water. Afterward, the samples were kept at room temperature and in the dark for 30 minutes, and their absorbance was subsequently read at a 515 nm wavelength using a spectrophotometer (UV-Vis array Spectrophotometer, Photonix-Ar2017, Iran). To prepare the control solution, all the steps of preparing the sample solution were repeated, only instead of the plant extract, 80% methanol (extract solvent) was used. The DPPH free radical inhibition percent was also obtained from the following equation ([Chen et al., 2013](#)).

Extraction and determination of essential oil

A water distillation system was used to obtain the amount of essential oil. After separation and dehydration by dry sodium sulfate, the essential oils were stored in dark glass containers at 4 °C until decomposition ([British Pharmacopoeia, 1980](#)).

2.9. Statistical analysis of data

The statistical data analysis of this experiment was performed using SAS 9.1 statistical software and the comparison of the treatment means was calculated using Duncan's multiple range test at the 5% level.

Results

Growth characteristics

Based on the comparison of the data means (Table 2), the highest plant height was observed in the red light treatment, and the lowest in the R50B50 light. The most fresh weight and dry weight of the shoots observed in the R70B30 light spectrum. Also, the lowest fresh weight and

dry weight of the shoots obtained in the blue light spectrum (Table 2). Besides, Leaf area were affected by light spectrum and the highest and lowest leaf area observed in the R70B30 and Red light light, respectively. On the other hand, the highest fresh and dry weight of roots obtained in the R70B30 and R50B50 light treatments. In this study, plant morphological and growth characteristics were significantly affected by different light spectra (Table 2).

Table 2. The effect of light on growth characteristics of *D. moldavica* plant

Light spectrum	Plant height (cm)	Biomass fresh weight (g)	Biomass dry weight (g)	Leaf area (cm ²)	Root fresh weight (mg)	Root dry weight (mg)
White	49.93 c	12.52 c	2.13 b	250.09 b	1.71 c	301.18 b
R70B30	65.50 b	16.24 a	2.91 a	351.14 a	2.84 a	520.68 a
Red	69.67 a	14.48 b	2.00 b	218.71 c	0.91 d	150.44 c
R30B70	44.33 d	10.79 d	1.95 b	271.67 b	2.32 b	352.40 b
Blue	46.83 cd	8.68 e	1.63 c	209.22 c	1.79 c	308.12 b
R50B50	36.33 e	10.82 d	2.12 b	265.67 b	2.83 a	506.08 a

Leaf Photosynthetic Pigment Amounts

The results showed that the amounts of chlorophyll a, chlorophyll b, and the sum of chlorophyll a and b in *D. moldavica* plants varied under different light spectra (Fig. 2). Comparison of the means between treatments showed that the highest amounts of chlorophyll a, b, and the sum of chlorophyll a and b were obtained in the R70B30 light environment and the lowest amounts were obtained in the blue light environment (Fig. 2). Consistent with these findings, in this study, the highest amounts of chlorophyll pigments were also observed in the combined red and blue light. In the present study, plants grown under the combined R70B30 light treatments had the highest amounts of photosynthetic pigments, which led to an increase in photosynthetic capacity and improved growth indices (Fig. 2).

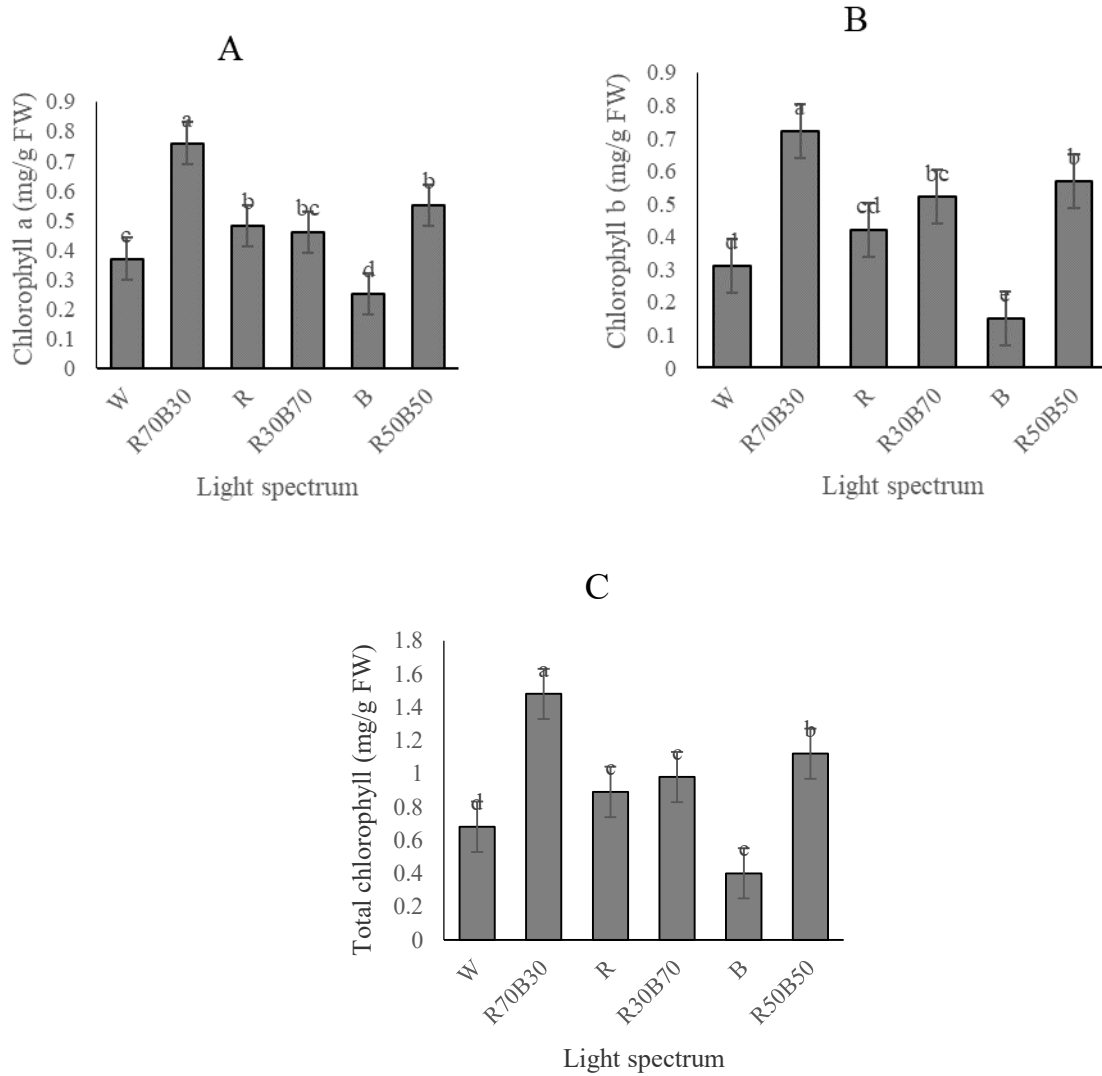
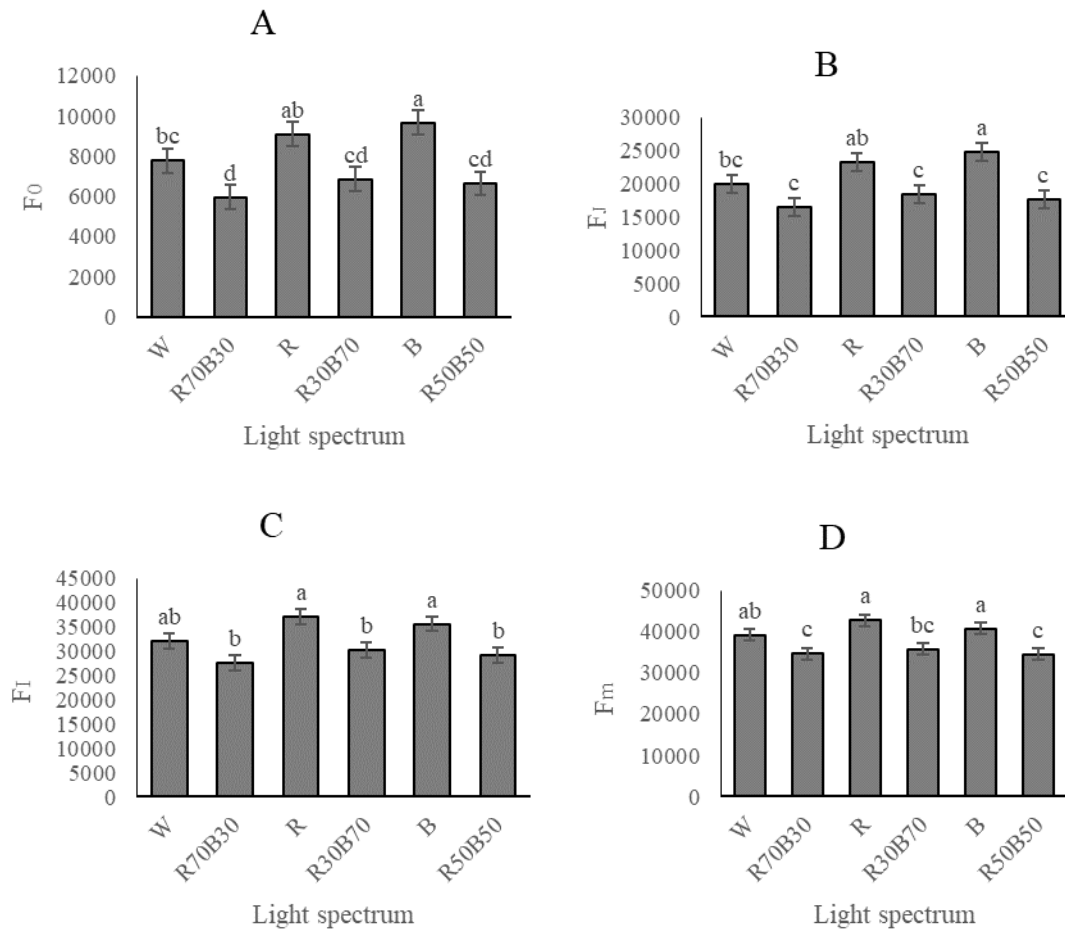


Figure. 2. Chlorophyll content in the *D. moldavica* plants.

Chlorophyll fluorescence

The results showed that in all four stages of the OJIP test, F_0 , F_1 , F_J and F_m , the highest fluorescence value belonged to red light and the lowest value belonged to the combined light of R501B50 and R70B30 (Fig. 3). The results of the mean comparison showed that the highest minimum fluorescence value (F_0) was in the red and blue light treatments and the lowest value belonged to the combined light of RB. The highest fluorescence value in two milliseconds (F_J) was reported in the red and blue light environments and no significant difference was observed among the other treatments. The highest fluorescence value in 60 milliseconds (F_1) was in red

light and its lowest value was in the combined light of R50B50 and R70B30, which of course did not differ significantly from white light. The highest maximum fluorescence value (F_m) was observed in the red light treatment and its lowest value in the combined light of RB. The highest amount of variable fluorescence (F_v) was observed in the red light treatment and the lowest amount was observed in the R50B50 treatment (Fig. 3). The red light treatment had the highest amount in all OJIP stage recording data with a significant difference from the other lights (Fig. 3).



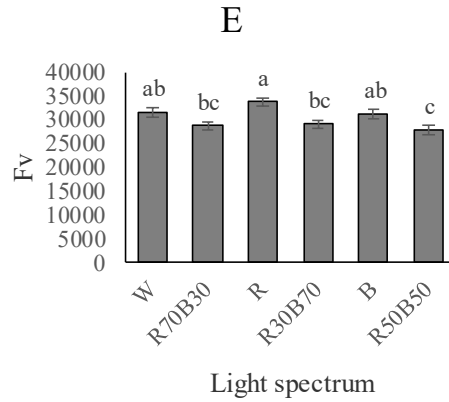


Fig. 3. O-J-I-P test contains of A) F_0 , B) F_J , C) F_I , D) F_m , and E) F_v in the *D. moldavica* plants (DMRT, $p \leq 0.05$)

Analysis of the results showed that different light spectra have a significant effect on the efficiency of the quantum yield of photosystem II (F_v/F_m or ΦP_0) (Fig. 4). According to the results of the comparison of the average data, the lowest value of the photosystem II quantum yield efficiency (F_v/F_m) was in single-spectrum blue and red lights and the highest value obtained in R70B30 and white light. The results showed that the efficiency of the photosystem II water splitting system was maximum under R70B30 and white light treatments and was minimum under single-spectrum red and blue light (Fig. 4). The decrease in F_v/F_m or ΦP_0 in red light can be due to the inactivation of the reaction center, which causes an increase in energy loss in the form of heat and fluorescence (Fig. 4).

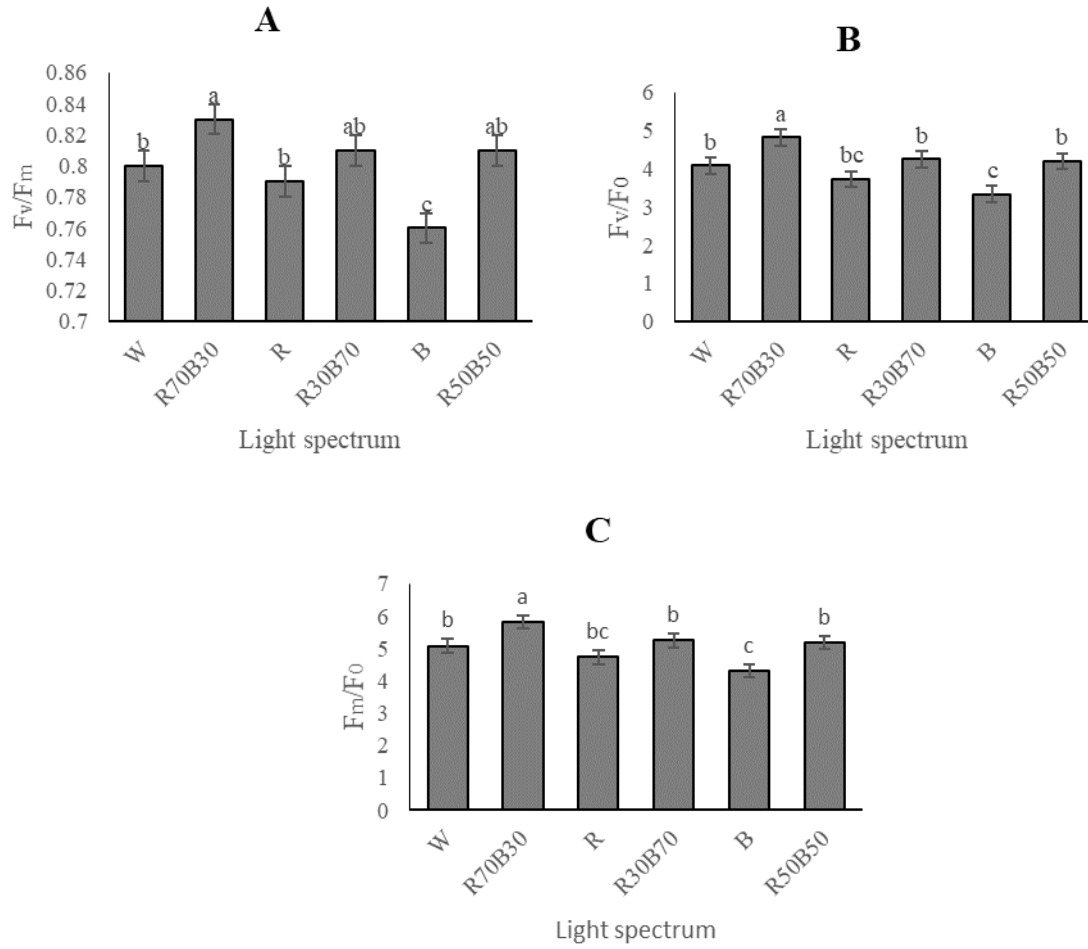


Fig. 4. O-J-I-P test contains of A) F_v/F_m ; B) F_v/F_0 , and C) F_m/F_0 in the *D. moldavica* plants (DMRT, $p \leq 0.05$)

Electron transport quantum efficiency indices

The results showed that the highest values of PI_{ABS} , Ψ_0 and ΦE_0 were observed in the R70B30 light treatment and the lowest values were observed in red and blue light. The highest values of ΦD_0 were observed in the red and blue light treatment and the lowest values belonged to R70B30 and white light (Fig. 5). High red light ratios increased these parameters, stating a decrease in photosynthetic efficiency with a decrease in the blue to red light ratio (Fig. 5).

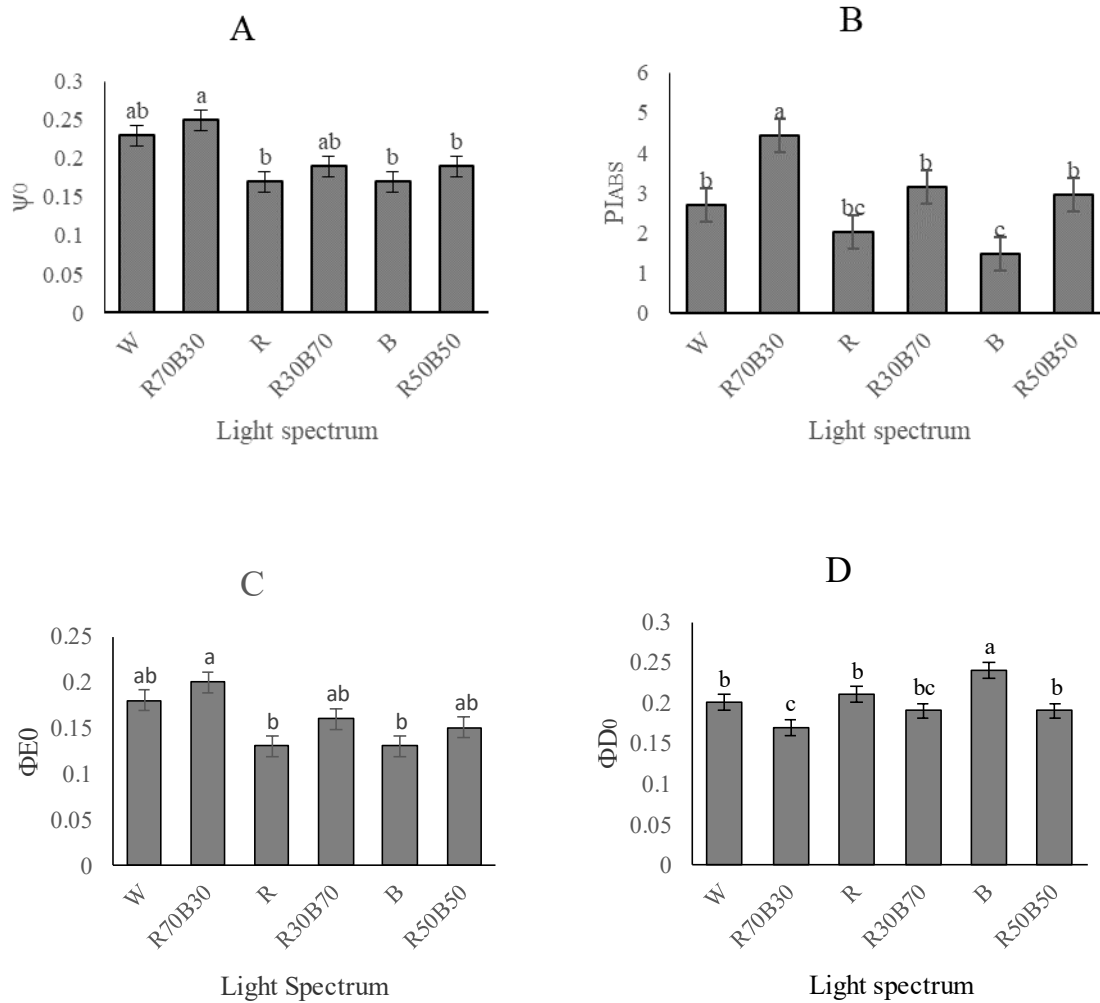


Fig. 5. A) Possibility that an electron travels further than QA (ψ_0), B) performance index in light absorption basis (PI_{ABS}), C) quantum yield of electron transport (Φ_{E0}), and D) Quantum yield of energy dissipation (ΦD_0) in the *D. moldavica* plants (DMRT, $p \leq 0.05$)

Specific energy fluxes (per photosystem II reaction center reducing quinone A)

Based on the results of the comparison of the mean data, the lowest ABS/RC value was observed in the R70B30 light treatment and no significant difference was observed in the other treatments (Fig. 6). The highest TR_0/RC was observed in the red light treatment and the lowest TR_0/RC was observed in the R70B30 light treatment (Fig. 6). The highest ET_0/RC and the lowest DI_0/RC were obtained in R70B30 light. Besides, there was no significant difference between the other treatments in terms of these two parameters (Figure 6).

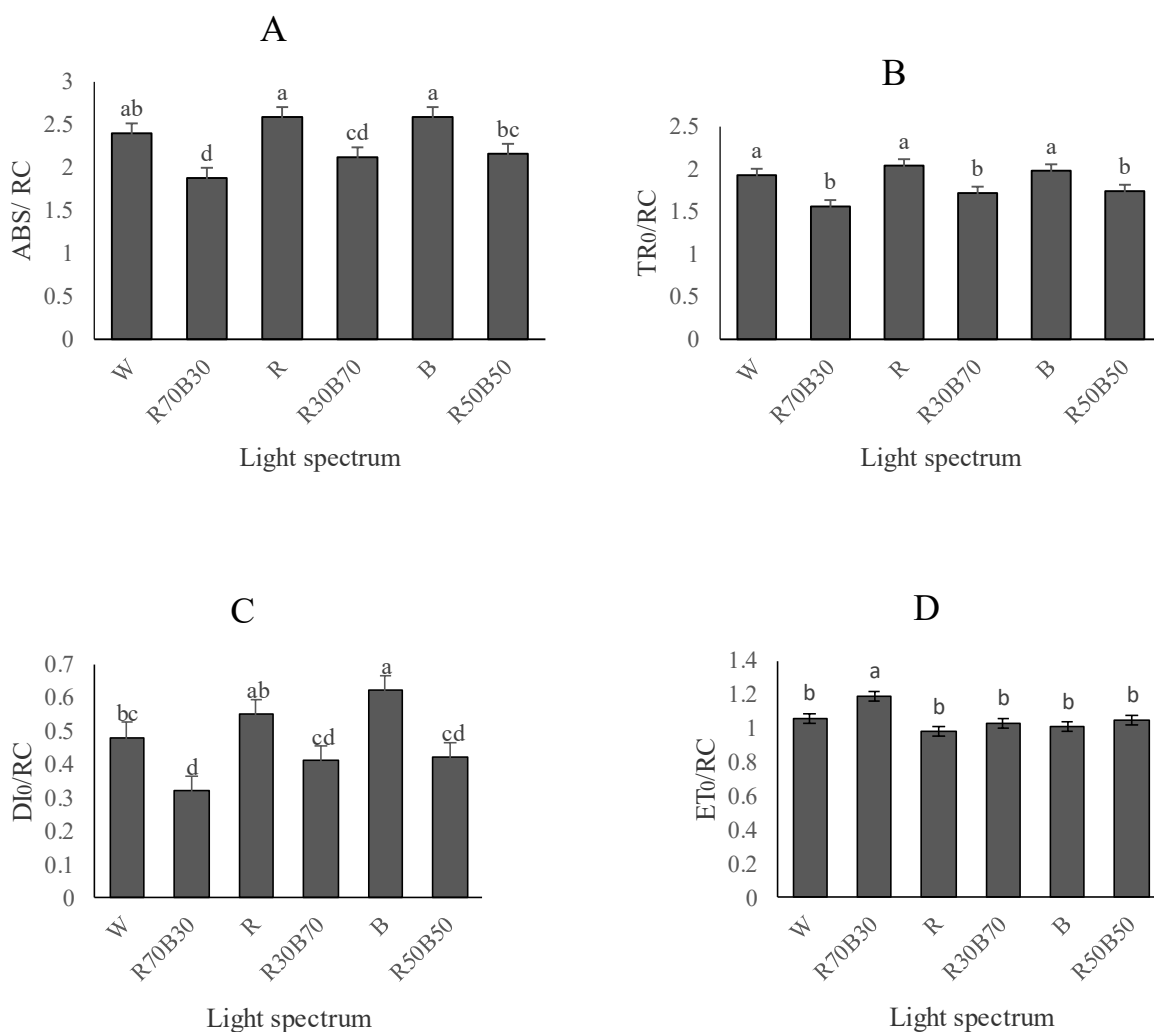


Fig. 6. Energy fluxes for A) ABS/RC, B) TR₀/RC, C) DI₀/RC, D) ET₀/RC in the *D. moldavica* plants (DMRT, $p \leq 0.05$)

Total phenol content

Different light spectra had significant differences in total phenol content (Fig. 7). The highest phenol content (130.26-136.94 μg gallic acid/g wet weight) was observed in the light environments of R50B50 and R70B30, respectively, and the lowest total phenol content (92.37-93.87 μg gallic acid/g wet weight) was observed in the treatments of R30B70 and red light. Different light spectra affect the expression of genes of some enzymes involved in the biosynthesis of secondary metabolites, leading to changes in the biochemical traits of the plant (Fig. 7).

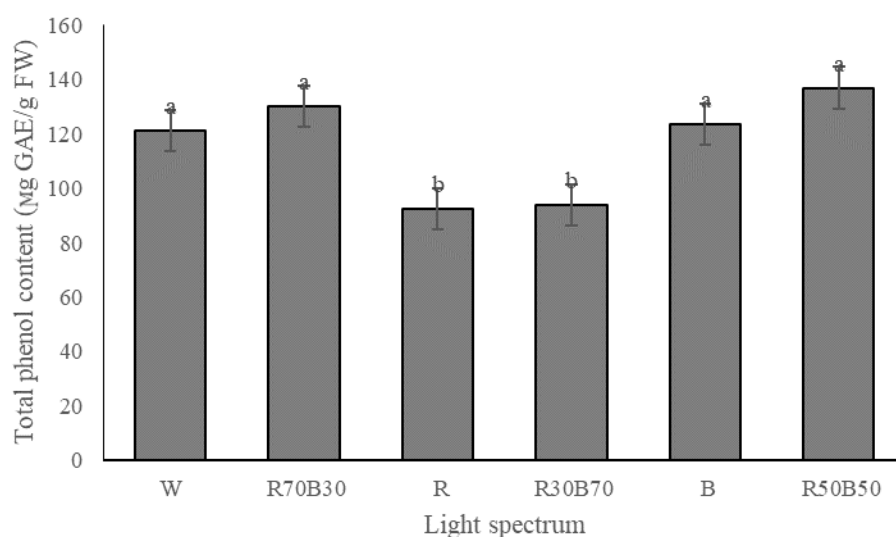


Fig.7. Total phenolic content in the *D. moldavica* plants grown under different light spectra with same intensity.

Antioxidant capacity

The highest antioxidant activity was observed under R70B30 and white light treatments (42.51 and 36.15 percent, respectively) and the lowest under red light (19.47 percent) (Fig. 8).

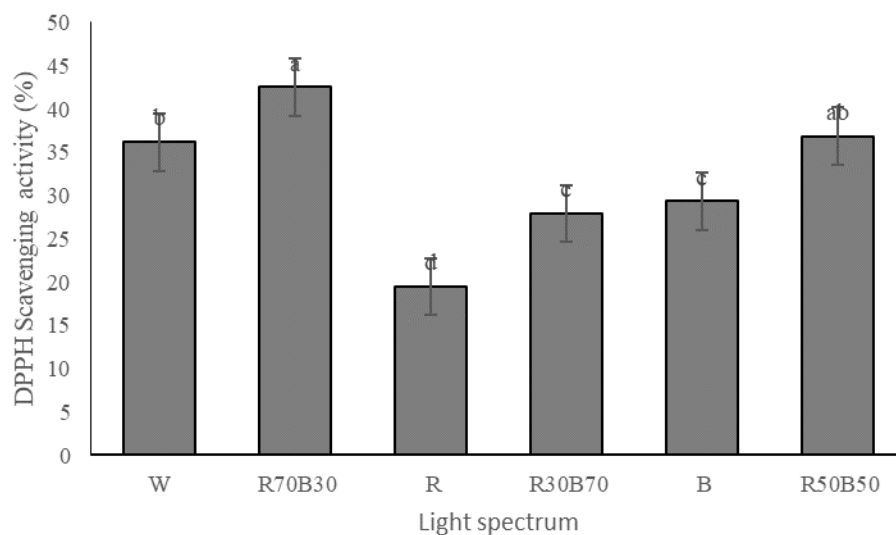


Fig. 8. Antioxidant activity in the *D. moldavica* plants grown under different light spectra with same intensity.

Essential oil percentage

The essential oil percentage of *D. moldavica* was significantly affected by light quality. In the present study, the essential oil content varied between 0.53 to 2.07 (Fig. 9). The highest essential oil content (2.07% v/w) was observed in the R70B30 light and the lowest essential oil content (0.53% v/w) was observed in plants grown under blue light. A comparison of the mean of the light treatments showed that the use of the R70B30 light treatment resulted in a 113.4% increase in the essential oil content compared to the white treatment (Fig. 9). In this study, it was observed that the optimal ratio of red and blue combined light had a greater effect on the essential oil content compared to the blue and red single-spectrum lights, which is probably due to the increased synthesis of secondary metabolites in this light environment (Fig. 9).

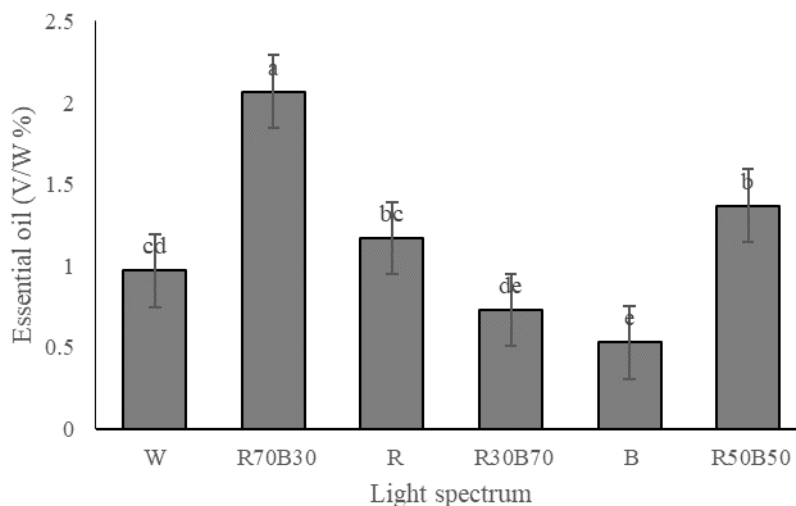


Fig. 9. The content of essential oil of *D. moldavica* plants. (DMRT, $p \leq 0.05$).

Discussion

Combined red and blue lights improved plant growth and performance indices compared to single-spectrum red and blue lights. Combined red and blue lights improved plant growth and performance indices compared to single-spectrum red and blue lights. Red and blue light contain the main wavelengths of light for plant growth and development (Kozai, 2016). Nania et al. (2012) stated that high blue light rates reduce height and biomass, and high red light rates increase height and biomass which is consistent with the results of this experiment. The reason for the increase in plant height with red light is due to changes in growth hormone levels. Red

and blue light affect stem elongation by changing the level of gibberellin in the plant ([Wang et al., 2015](#)). It has been reported that red light generally increases plant growth by increasing fresh and dry weight, height, and leaf area of plants. While blue light affects photosynthetic performance, chlorophyll formation, and chloroplast development, rather than directly affecting biomass ([Savvides et al., 2011](#)). It has been proven that the combination of red and blue light can affect the amount of photosynthetic pigments ([Wang et al., 2016](#)). [Hosseini et al. \(2019\)](#) reported an increase in photosynthetic pigment production, electron transport efficiency, and growth indices of green and purple basil varieties under the influence of combined red and blue light. In accordance with these findings, in this study, the highest amount of chlorophyll pigments was observed under combined red and blue light. Light spectrum and intensity straightly efficacy on photosynthetic reactions. High F_0 indicates that photosystems are not functioning properly and reaction centers are closed ([Strasser et al., 2000](#)). High F_0 is attributed to the deterrence of the reaction centers of photosystem I, which prevents electron transmission from QA to QB, thereby reducing the energy-trapping performance in photosystem I ([Falqueto et al., 2017](#)). Several studies have reported the lack of optimal plant development, the creation of light damage in leaves, damage escape reactions in photosystems ([Ouzounis et al., 2015](#); [Nozue and Masao, 2018](#)). The higher mean fluorescence and maximum fluorescence in red light compared to other lights suggests that a greater proportion of photons are reflected in this light, which could indicate chlorophyll degradation and permanent damage to electron acceptors. However, the lower fluorescence at different stages in the combined red and blue lights indicates better health and efficiency of the photosynthetic system in these two lights ([Hogewoning et al., 2010](#)). Photoinhibition caused by various conditions can have an adverse effect on the functioning of photosystem II and lead to limiting photosynthetic capacity ([Zlatev and Yordanov, 2004](#)). A decrease in the F_v/F_m index indicates a decrease in the photochemical efficiency of photosystem II and damage to the photosynthetic apparatus ([Shu et al., 2013](#)). Studies have shown that when plants are exposed to red light for a long time, leaf photosynthesis is severely impaired. The occurrence of red light syndrome in plants grown under red light in this study was clearly evident both morphologically (creating epinasty and leaf deformities) and in terms of photosynthesis and function. At the same time, low F_v/F_m ratio is also associated with the phenomenon of red light syndrome ([Hogewoning et al., 2010](#)). The increase in the energy loss quantum yield (ΦD_0) in plants grown under red light conditions confirms these findings. In confirmation of these

findings, Zheng and Van Labeke (2018) reported a decrease in F_v/F_m and electron transfer quantum efficiency in photosystem II in plants grown under red light. Energy conversion into heat is a response by the plant to protect cells from light-induced damage. In accordance with our findings, it has been reported that red light causes a decrease in F_v/F_m and an increase in energy loss from the plant (Aliniaieifard et al., 2018). Chen et al. (2013) also stated that the decrease in F_v/F_m by red light was due to a decrease in photochemical activity due to the inactivation of PSII reaction centers and damage to the D1 protein. The photosynthetic capacity of spinach leaves grown under red and blue combined light conditions was higher than that of plants exposed to single-spectrum red light, and the existence of blue and red light is essential to increase net photosynthesis, and this is if the amount of red light is at least 70% of the total final irradiance intensity, which is the same as the findings of this research (Matsuda et al., 2008). The efficiency of the water splitting system II (F_v/F_0) is very sensitive indicators of photosynthetic potential in stressed and healthy plants (Ozfidan et al., 2013). A decrease in this parameter is a clear indication that photosynthetic efficiency and the electron transport chain are affected (Shu et al., 2013). Accordingly, an increase in ΦD_0 in plants grown under R light has been reported in basil (Hosseini et al., 2019), marigold (Aliniaieifard et al., 2018) and chrysanthemum (Seif et al., 2019). The PI_{ABS} index represents the energy transferred from photosystem II to photosystem I (Strasser et al., 2010). According to the results of the quantum efficiency indices for electron transfer, it can be concluded that plants grown under mixed R70B30 light exhibit better photosynthetic performance (Fig. 5), which is consistent with the research of Hosseini et al. (2019). PI_{ABS} combines energy flows from the initial stage of the absorption process to the reduction of plastoquinone (Strasser et al., 2000). Under abiotic stresses, PI_{ABS} is the most delicate factor for measuring photosynthetic performance (Bayat et al., 2018). The decrease in the rate of PI_{ABS} in red light is due to the high absorption of light energy (ABS/RC), the electron trapping flux per reaction center (TR_0/RC), the energy dissipated per reaction center (DI_0/RC), and the reduction in electron transfer per reaction center (ET_0/RC). ΦE_0 is a parameter that indicates the rate of electron flow to the amount of energy absorbed. In other words, the aforementioned index indicates the probability of electron transfer to carriers after QA^- by the absorbed photon energy. This index increased in plants grown under mixed red and blue light and decreased in plants grown under single-spectrum red and blue light. A decrease in this parameter means a decrease in the rate of electron flow towards forward carriers in the electron

transport pathway (Mehta et al., 2010). A decrease in this parameter can also be considered a result of a decrease in Ψ_0 (the probability of electron transfer across QA⁻) (Goncalvez, 2007). The decrease in PIABS also indicates that the system structure, potential PSII activity, and the damage-repair ratio of the D1 protein in PSII may be compromised or unable to progress under certain fully light conditions (Gasulla et al., 2019). High levels of ABS/RC have also been showed in plants grown under red light conditions (Aliniaiefard et al., 2018; Hosseini et al., 2019). So, to hold natural photosynthesis efficiency, a specific proportion of blue to red light in the overall spectra is necessary (Hogewoning et al., 2010). DI₀/RC is a parameter related to the energy dissipated per reaction center in the photosystem II, which indicates the efficiency of non-photochemical excitation processes (Falqueto et al., 2017). In the present study, the lowest value of DI₀/RC was observed in plants grown under R70B30 light (Fig. 6), which is consistent with the results of Bayat et al. (2018). The increase in this parameter indicates the shutdown of some of the photosystem II reaction centers, which consequently leads to a decrease in the QA reduction capability and most of the light absorbed by the photosystems is not used for the photochemical efficiency of the electron transport chain and is dissipated as heat from the electron transport system (Veiga et al., 2013). The reduction in Fv/Fm usually happen when PSII function and structure are disturbed by stress, causing more of the light energy absorbed from the PSII reaction center to be wasted (Gasulla et al., 2019). The increase in phenolic and flavonoid compounds in plants may be due to the increased activity of enzymes related to the synthesis of these compounds (Meng et al., 2004). Also, the increase in the levels of these compounds by light may be related to the increased production of Coumaroyl-CoA and Malonyl-CoA, which act as substrates for the biosynthesis of phenolic compounds (Kim et al., 2006). Several studies have shown that the use of single-spectrum or combined blue light (RB) increases secondary metabolites such as phenolics (Verma et al., 2012). Blue light increases phenolic compounds by increasing the activity of the enzyme phenylalanine ammonia lyase (a key enzyme in the phenylpropanoid pathway) (Connor et al., 2005). According to the findings of this study, the highest amount of phenolic compounds was observed in green basil, gourd, rose and chrysanthemum under combined RB light (Iwai et al., 2010; Ouzounis et al., 2014). The highest antioxidant capacity was reported in *Rhodiola imbricata* under the white light spectrum (Kapoor et al., 2018). Ren et al. (2015) investigated the effect of different LED light ratios on *Gynura bicolor* and found that increasing the amount of blue light from 15% to 30% led to an increase in

antioxidant capacity. Also, the highest antioxidant activity, total phenols and anthocyanins were observed in two basil varieties under RB light treatment (70:30) ([Hosseini et al., 2019](#)), which is consistent with the results of this study. In peppermint, spearmint and oregano, the essential oil content under red light was 39% and 86% higher than that under blue and white light, respectively ([Dou et al., 2017](#)). [Park et al. \(2013\)](#) reported that in ginseng, blue light led to an increase in the compounds vanillic acid, coumaric acid, and ferulic acid. In general, the results indicate the effect of light spectra on the production of secondary metabolites in plant species, and it seems likely that these wavelengths are associated with the activation of some plant genes that are ultimately responsible for the increase in plant secondary metabolites ([Sabzalian et al., 2014](#)).

Conclusion

The highest amount of chlorophyll pigments, total phenol content, and antioxidant activity was obtained in plants grown in mixed red and blue light environments (especially R70B30). A combination of red and blue light has the greatest effect on plant growth and the biosynthesis of secondary metabolites, as it is the primary energy source for photosynthetic carbon dioxide absorption in plants. According to the results of this study, single-spectrum red and blue lights are not suitable for the growth and production of secondary metabolites. The highest biochemical, photosynthetic, growth, and functional indices were observed in mixed RB light environments.

Data availability

Data will be made available on request.

References

1. Aalifar, M., Aliniaiefard, S., Arab, M., Zare Mehrjerdi, M., Dianati Daylami, S., Serek, M., Woltering, E. & Li, T. Blue light improves vase life of carnation cut flowers through its effect on the antioxidant defense system. *Front. Plant Sci.* **11**, 511 (2020). <https://doi.org/10.3389/fpls.2020.00511>
2. Acimovic, M., Šovljanski, O., Šeregelj, V., Pezo, L., Zheljaskov, V.D. & Ljubic, J. Chemical composition, antioxidant, and antimicrobial activity of *Dracocephalum moldavica* L. essential oil and hydrolate. *Plants.* **11**, 941 (2022). <https://doi.org/10.3390/plants11070941>

3. Aćimović, M., Sikora, V., Brdar-Jokanović, M., Kiproviski, B., Popović, V. & Koren, A. *Dracocephalum moldovica*: Cultivation, chemical composition, and biological activity. *J. Agron. Technol. Eng. Manag.* **2**, 153-167 (2019).
4. Aliniaiefard, S., Seif, M., Arab, M., Zare Mehrjerdi, M., Li, T. & Lastochkina, O. Growth and photosynthetic performance of *Calendula officinalis* under monochromatic red light. *Int. j. hortic. sci. technol.* **5**, 123-132 (2018).
<https://doi.org/10.22059/ijhst.2018.261042.248>
5. Amin, T., Chauhan, R., Varma, A. & Tiwari, A. *Dracocephalum moldavica* L.: A review on its traditional uses, phytochemistry, and pharmacological properties. *J. Ethnopharmacol.* **254**, 112490 (2020).
6. Amiri, A., Kafi, M., Kalate-Jari, S. & Matinizadeh, M. Tulip response to different light sources. *J. Anim. Plant Sci.* **28**, 539-545 (2018).
7. Bayat, L., Arab, M., Aliniaiefard, S., Seif, M., Lastochkina, O. & Li, T. Effects of growth under different light spectra on the subsequent high light tolerance in rose plants. *AoB Plants.* **10** (5), 1-17 (2018). <https://doi.org/10.1093/aobpla/ply052>
8. British Pharmacopoeia. *H.M.S. Office. 2, London.* 109-110 (1980)
9. Chen, S., Shen, X., Cheng, S., Li, P., Du, J., Chang, Y. & Meng, H. Evaluation of garlic cultivars for polyphenolic content and antioxidant properties. *PLoS One.* **8** (11), 1-12 (2013). <https://doi.org/10.1371/journal.pone.0079730>
10. Connor, A.M., Finn, C.E. & Alspach, P.A. Genotypic and environmental variation in antioxidant activity and total phenolic content among blackberry and hybrid berry cultivars. *J. Am. Soc. Hortic. Sci.* **30**(4): 527-533 (2005).
<http://doi.org/10.21273/JASHS.130.4.527>
11. Falqueto, A.R., Da Silva Júnior, R.A., Gomes, M.T.G., Martins, J.P.R., Silva, D.M. & Partelli, F.L. Effects of drought stress on chlorophyll a fluorescence in two rubber tree clones. *Sci Hort.* **224**, 238-243 (2017). <https://doi.org/10.1016/j.scienta.2017.06.019>
12. Gasulla, F., Casano, L. & Guéra, A. Chlororespiration induces non-photochemical quenching of chlorophyll fluorescence during darkness in lichen chlorobionts. *Physiol. Plants.* **166**, 538-552 (2019). <https://doi.org/10.1111/ppl.12792>
13. Ghorbanzadeh, P., Aliniaiefard, S., Esmaeili, M., Mashal, M., Azadegan, B. & Seif, M. Dependency of growth, water use efficiency, chlorophyll fluorescence, and stomatal

- characteristics of lettuce plants to light intensity. *Plant Growth Regul.* **40(5)**, 2191-2207 (2020). <http://doi.org/10.1007/s00344-020-10269-z>
14. Goncalves, J.F.C., Santos, U.M., Nina, A. & Chevreuil, L.R. Energetic flux and performance index in copaiba (*Copaifera multijuga Hayna*) and mahogany (*Swietenia macrophylla King*) seedling grown under two irradiance environments. *Braz. J. Plant Physiol* **19**, 171-184 (2007). <http://doi.org/10.1590/S1677-04202007000300001>
 15. Hogewoning, S.W., Trouwborst, G., Maljaars, H., Poorter, H., van Ieperen, W. & Harbinson, J. Blue light dose-responses of leaf photosynthesis, morphology, and chemical composition of *Cucumis sativus* grown under different combinations of red and blue light. *J Exp Bot* **1**, 3107–3117 (2010). <http://doi.org/10.1093/jxb/erq132>
 16. Hosseini, A., Mehrjerdi, M.Z., Aliniaiefard, S. & Seif, M. Photosynthetic and growth responses of green and purple basil plants under different spectral compositions. *Physiol Mol Biol Plants* **25**, 741-752 (2019). <https://doi.org/10.1007/s12298-019-00647-7>
 17. Huber, M., Nieuwendijk, N.M., Pantazopoulou, C.K. & Pierik, R. Light signalling shapes plant–plant interactions in dense canopies. *Plant Cell Environ* **44**, 1014-1029 (2021). <https://doi.org/10.1111/pce.13912>
 18. Kapoor, S., Raghuvanshi, R., Bhardwaj, P., Sood, H., Saxena, S. Chaurasia, O.P. Influence of light quality on growth, secondary metabolites production and antioxidant activity in callus culture of *Rhodiola imbricata* Edgew. *J. Photochem Photobiol B.* **183**, 258-265 (2018). <https://doi.org/10.1016/j.jphotobiol.2018.04.018>
 19. Iwai, M., Ohta, M., Tsuchiya, H. & Suzuki, T. Enhanced accumulation of caffeic acid, rosmarinic acid and luteolin-glucoside in red perilla cultivated under red diode laser and blue LED illumination followed by UV-A irradiation. *J. Funct. Foods* **2(1)**, 66-70 (2010). <https://doi.org/10.1016/j.jff.2009.11.002>
 20. Kim, E.H., Kim, S.H., Chung, J.I., Chi, H.Y., Kim, J.A. & Chung, I.M. Analysis of phenolic compounds and isoflavones in soybean seeds (*Glycine max L.*) and sprouts grown under different conditions. *Eur. Food Res. Technol* **22 (2)**, 201-208 (2006). <https://doi.org/10.1007/s00217-005-0153-4>
 21. Kim, H.J., Lin, M.Y. & Mitchell, C. A. Light spectral and thermal properties govern biomass allocation in tomato through morphological and physiological changes. *Environ. Exp. Bot.* **157**, 228-240 (2019). <http://doi.org/10.1016/j.envexpbot.2018.10.019>

22. Klem, K., Gargallo-Garriga, A., Rattanapichai, W., Oravec, M., Holub, P., Veselá, B., Sardans, J., Peñuelas, J. Urban, O. Distinct morphological, physiological, and biochemical responses to light quality in barley leaves and roots. *Front. Plant Sci.* **10**, 1026 (2019). <https://doi.org/10.3389/fpls.2019.01026>
23. Kozai, T. Why LED Lighting for Urban Agriculture? In: Kozai, T., Fujiwara, K. Runkle, E.S., Eds., *LED Lighting for Urban Agriculture*, Springer, Singapore. 4-10 (2016). <https://doi.org/10.1007/978-981-10-1848-0>
24. Lichtenthaler, H.K. & Wellburn, A.R. Determinations of total carotenoids and chlorophylls a and b of leaf extracts in different solvents. *Biochem Soc Trans.* **603**, 591-592 (1983). <https://doi.org/10.1042/bst0110591>
25. Matsuda, R., Ohashi-Kaneko, K., Fujiwara, K. & Kurata, K. Effects of blue light deficiency on acclimation of light energy partitioning in PSII and CO₂ assimilation capacity to high irradiance in Spinach leaves. *Plant, Cell Physiol.* **49**, 664-670 (2008). <http://doi.org/10.1093/pcp/pcn041>
26. Mehta, P., Jajoo, A., Mathur, S. & Bharti, S. Chlorophyll a fluorescence study revealing effects of high salt stress on photosystem II in wheat leaves. *Plant Physiol Biochem.* **48**, 16-20 (2010). <https://doi.org/10.1016/j.plaphy.2009.10.006>
27. Meng, X., Xing, T. & Wang, X. The role of light in the regulation of anthocyanin accumulation in *Gerbera hybrida*. *Plant Growth Regul.* **44** (3), 243-250 (2004). <https://doi.org/10.1007/s10725-004-4454-6>
28. Naznin, M., Lefsrud, M., Gravel, V. & Aza, M. Blue light added with red LEDs enhance growth characteristics, pigments content, and antioxidant capacity in lettuce, spinach, kale, basil, and sweet pepper in a controlled environment. *Plants.* **8**, 93 (2019). <https://doi.org/10.3390/plants8040093>
29. Nozue, H., Masao, G. Usefulness of Broad-Spectrum White LEDs to Envision Future Plant Factory. In: Kozai, T. (Ed), *Smart Plant Factory, The Next Generation Indoor Vertical Farms*. Springer Nature Singapore. 197-210 (2018).
30. Ouzounis, T., Fretté, X., Rosenqvist, E. & Ottosen, C.O. Spectral effects of supplementary lighting on the secondary metabolites in roses, chrysanthemums, and campanulas. *J. Plant Physiol.* **171**, 1491-1499 (2014). <http://doi.org/10.1016/j.jplph.2014.06.012>

31. Ouzounis, T., Rosenqvist, E. & Ottosen, C. Spectral Effects of Artificial Light on Plant Physiology and Secondary Metabolism: A Review. *HortSci.* **50(8)**, 1128-1135 (2015). <http://dx.doi.org/10.21273/HORTSCI.50.8.1128>
32. Ozfidan, C., Turkan, I., Sekmen, A.H. & Seckin, B. Time course analysis of ABA and non-ionic osmotic stress-induced changes in water status, chlorophyll fluorescence and osmotic adjustment in *Arabidopsis thaliana* wild-type (Columbia) and ABA deficient mutant (*aba2*). *Environ. Exp. Bot.* **86**, 44-51 (2013). <https://doi.org/10.1016/j.envexpbot.2010.09.008>
33. Park, S.Y., Lee, J.G., Cho, H.S., Seong, E.S., Kim, H.Y., Yu, C.Y. & Kim, J.K. Metabolite profiling approach for assessing the effects of colored light-emitting diode lighting on the adventitious roots of ginseng (*Panax ginseng* C. A. Mayer). *Plant Omics J.* **6**, 224-230 (2013).
34. Ren, J., Guo, S., Xu, C., Yang, C., Ai, W., Tang, Y. & Qin, L. Effects of different carbon dioxide and LED lighting levels on the anti-oxidative capabilities of *Gynura bicolor*. *Adv. Space Res.* **3 (2)**, 353-361 (2015). <http://doi.org/10.1016/j.asr.2013.11.019>
35. Sabzalain, M.R., Heydarizadeh, P., Zahedi, M., Boroomand, A., Agharokh, M., Sahba, M.R & Schoefs, B. High performance of vegetables, flowers, and medicinal plants in a red-blue LED incubator for indoor plant production. *Agron. Sustain. Dev* **34**, 879-886 (2014). <http://doi.org/0.1007/s13593-014-0209-6ff>
36. Savvides, A., Fanourakis, D & Van Ieperen, W. Co-ordination of hydraulic and stomatal conductances across light qualities in cucumber leaves. *J. Exp. Bot.* **63**, 1135-1143 (2012). <http://doi.org/10.1093/jxb/err348>
37. Seif, M., Aliniaiefard, S., Arab, M., Mehrjerdi, M.Z., Shomali, A., Fanourakis, D., Li, T. & Woltering, E. Monochromatic red light during plant growth decreases the size and improves the functionality of stomata in chrysanthemum. *Funct. Plant Biol.* **48**, 515-528 (2021). <http://doi.org/10.1071/FP20280>
38. Shu, S., Yuan, L.Y., Guo, S.R., Sun, J. & Yuan, Y.H. Effects of exogenous spermine on chlorophyll fluorescence, antioxidant system and ultrastructure of chloroplasts in *Cucumis sativus* L. under salt stress. *Plant Physiol Biochem.* **63**, 209-216 (2013). <https://doi.org/10.1016/j.plaphy.2012.11.028>

39. Strasser, R.J., Srivastava, A., Tsimilli-Michael, M. The fluorescence transient as a tool to characterize and screen photosynthetic samples. *In Probing Photosynthesis: Mechanisms, Regulation and Adaptation*; CRC Press: Boca Raton, FL, USA. 445-483 (2000).
40. Strasser, R.J., Tsimilli-Michael, M., Qiang, S. & Goltsev, V. Simultaneous in vivo recording of prompt and delayed fluorescence and 820-nm reflection changes during drying and after rehydration of the resurrection plant *Haberlea rhodopensis*. *Biochimica et Biophysica Acta (BBA)-Bioenergetics* **1797** (6-7), 1313-1326 (2010). <https://doi.org/10.1016/j.bbabi.2010.03.008>
41. Veiga, T.A.M., King-Díaz, B., Marques, A.S.F., Sampaio, O.M., Vieira, P.C. & Lotina-Hennsen, B. Furoquinoline alkaloids isolated from *Balfourodendron riedelianum* as photosynthetic inhibitors in spinach chloroplasts. *J. Photochem. Photobiol. B: Biol.* **120**, 36-43 (2013). <https://doi.org/10.1016/j.jphotobiol.2013.01.006>
42. Verma, R.S., Padalia, R.C. & Chauhan, A. Variation in the volatile terpenoids of two industrially important basil (*Ocimum basilicum* L.) cultivars during plant ontogeny in two different cropping seasons from India. *J. Sci. Food Agric.* **92** (3), 626-631 (2012). <http://doi.org/10.1002/jsfa.4620>
43. Wang, X., Xu, X. & Cui, J. The importance of blue light for leaf area expansion, development of photosynthetic apparatus, and chloroplast ultrastructure of *Cucumis sativus* grown under weak light. *Photosyn.* **53**, 213-222 (2015). <http://doi.org/10.1007/s11099-015-0083-8>
44. Wang, J., Lu, W., Tong, Y. & Yang, Q. Leaf morphology, photosynthetic performance, chlorophyll fluorescence, stomatal development of lettuce (*Lactuca sativa* L.) exposed to different ratios of red light to blue light. *Front. Plant Sci.* **7**, 250 (2016). <http://doi.org/10.3389/fpls.2016.00250>
45. Zheng, L. & Van Labeke, M.C. Effects of different irradiation levels of light quality on *Chrysanthemum*. *Sci. Hortic.* **233**, 124-131 (2018). <http://doi.org/10.1016/j.scienta.2018.01.033>
46. Zlatev, Z.S. & Yordanov, I.T. Effects of soil drought on photosynthesis and chlorophyll fluorescence in bean plants. *Bulgar. J. Plant Physiol.* **30**, 3-18 (2004).
47. Zotov, V.S., Bolychevtseva, Y.V., Khapchaeva, S.A., Terekhova, I.V., Shubin, V.V., Yurina, N.P. & Kulchin, Y.N. Effect of Light Quality on the Biomass Yield, Photosystem

2 Fluorescence, and the Total Essential Oil Content of *Ocimum basilicum*. *App. Biochem. Microbiol.* **56 (3)**, 336-343 (2020). <http://doi.org/10.1134/S1021443723600794>

48. Zuk-Gołaszewska, K., Upadhyaya, M.K. & Gołaszewski, J. The effect of UV-B radiation on plant growth and development. *Plant Soil Environ.* **49**, 135-140 (2003).

Acknowledgments

This work has been financially supported by the vice-chancellor for research of University of Torbat-e Jam.

Author contributions

Dr. Hossein Nastari Nasrabadi : Conceptualization, Investigation, Data curation, Data analysis, Writing – review & editing. Dr. Mahboubeh Zamanipour: Conceptualization, Supervision, Formal analysis, Writing. Dr. Mahdi Moradi: Investigation, Data curation

Funding

This work was supported by the Torbat-e Jam University [grant number TP-140311].

Declarations

Competing interests

The authors declare no competing interests.