Research paper

Effects of LED Light Quality on the Physiology and Morphological Structure of *Camellia oleifera* Leaves

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【Summary】

Light quality is an important factor in plant growth and development. *Camellia oleifera* is a tree with a high economic value, and the effects of light quality on *C. oleifera* have not been adequately researched. Therefore, this study explored the effects of light quality on physiological parameters and the morphological structure of *C. oleifera* leaves. Light treatments with four light-emitting diodes (LEDs) were set: blue (B), red (R), white (W, the control group), and a combination of red and blue light (RB). Results showed that the net photosynthetic rate (P_n), maximum net photosynthetic rate ($P_{n\text{-}max}$), and stomatal conductance (G_s) of mature leaves under treatment B were significantly higher than those under W, those of treatment R were considerably lower than those of W, while those of treatment RB were higher than those of W but lower than those of treatment B. Bud numbers were markedly higher in treatment B than in W, and strikingly lower in treatment R than in W. The number of stomata increased under treatment RB, whereas stomatal size increased under treatment B. Palisade and spongy tissues developed normally under B and RB treatments, while leaves were thinner under R and W and palisade tissue was not obvious. In conclusion, red light is not conducive to the growth and development of *C. oleifera*, but blue light can effectively promote its growth. Thus, blue LED lights can be used as an auxiliary light source for growing and strengthening *C. oleifera* seedlings.

Key words: Camellia oleifera, leaf anatomical structure, light quality, photosynthesis, stomata.

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研究報告

發光二極體光質對油茶葉片生理特徵及型態構造之影響

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摘 要

光質是影響植物生長發育的重要因素。油茶是一種具高經濟價值的樹木，至今仍未有充分研究其光質的影響。因此，本研究探討了光質對油茶幼苗形態結構和生理參數的影響。設置了四種發光二極體(LED)的光處理：藍光(B)、紅光(R)、白光(W)和紅藍混合光(RB)。結果表明B處理的淨光合速率(P_n)、最大淨光合效率($P_{n\text{-}max}$)、氣孔導度(G_s)和芽數量均顯著高於W，R處理均顯著低於W，RB處理高於W但低於B處理。B處理芽數量顯著高於W，R處理顯著低於W。紅藍光下氣孔數量增加，藍光下氣孔變大。在B和RB處理下，柵欄組織和海綿組織正常發育，紅光和白光下葉片較薄且柵欄組織不明顯。綜上所述，紅光不利於油茶生長發育，藍光能有效促進油茶生長。因此，藍色LED光是促進油茶生長壯苗的最佳輔助光源。

關鍵詞：油茶、光質、葉片解剖結構、光合作用、氣孔。

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INTRODUCTION

Camellia oleifera is native to China (Gao et al. 2017). The seeds of this tree are used to extract tea oil, a rich source of unsaturated fatty acids and a healthy and popular cooking oil. Light is the most important factor for plant growth and development (Lv et al. 2020). During photosynthesis, plants utilize sunlight, CO_2, and water to synthesize carbohydrates (Heyneke and Fernie 2018). Several studies indicated that plant growth and development are influenced by light quality and intensity (Shafiq et al. 2021). Light quality can regulate the number of buds by regulating the distribution of nutrients and the response of photoreceptors (Leduc et al. 2012). The bud is the basis of plant growth and development, and the number of buds can profoundly affect plant growth, physiology, and biomass (Mckown et al. 2016). Light quality can alter the accumulation of nutrients; for instance, the net photosynthetic rate (P_n), starch content, and sugar content of tomato seedlings under red and blue light were significantly higher than those of seedlings under other light quality treatments (Li et al. 2017). Soybean seedlings had the highest chlorophyll *b* and total chlorophyll contents under red light but a lower photosynthetic capacity for growth and development (Fang et al. 2021). *Campomanesia pubescens* seedlings produced higher stomatal density, stomatal conductance, and chlorophyll fluorescence parameters under red and blue light (Centofante 2020). The leaf thickness of Oriental plane (*Platanus orientalis* L.) strikingly increased under red and blue light, whereas that of tomato significantly decreased (Arena et al. 2016). Plant growth rates are mainly restricted by nitrogen, and

are also affected by light and phosphorus after the nitrogen restriction is removed (Sims et al. 2012). Therefore, light quality has an important effect on a plant's photosynthetic capacity, material accumulation, and shape. Appropriate light quality can benefit seedlings, and obtaining stronger buds can produce more scions for grafting. There is a dearth of research on the effects of light on *C. oleifera* seedlings.

Plants mainly absorb blue-violet and red light; in this study, red, blue, and red and blue mixed light-emitting diodes (LEDs) were used as light sources for *C. oleifera* seedlings, and white light was used as a control. It was found that red-blue mixed light could increase the multiplication coefficient of *C. oleifera* plantlets, and produced significant changes in the morphological structure, stomatal density and size, and chlorophyll contents (He et al. 2020). In this study, stomatal morphology, the leaf anatomical structure, and chlorophyll contents of *C. oleifera* were analyzed in addition to the effects of light quality on growth, photosynthetic parameters, and nutrition-related indexes. This study provides a theoretical basis for cultivating high-quality *C. oleifera* seedlings under protected cultivation.

MATERIALS AND METHODS

Plant materials and growth conditions

Experiments were conducted in 2021 in a greenhouse without natural light at the Key Laboratory of the Ministry of Education for the Cultivation and Protection of Economic Forestry of the Central South Univ. of Forestry and Technology, Changsha, China. Three-year-old *C. oleifera* seedlings were used as test materials.

The experiment included four different light quality treatments: blue light (B), white light (W), red light (R), and red and blue light combination (RB; red and blue at a 1:1 ratio). Spectral characteristics of the different light quality treatments (Fig. 1) were measured with a HopooColor OHSP-350SF Spectral Color Luminance Meter (HopooColor, Hangzhou, China). Five *C. oleifera* seedlings were planted in each treatment, and all treatments

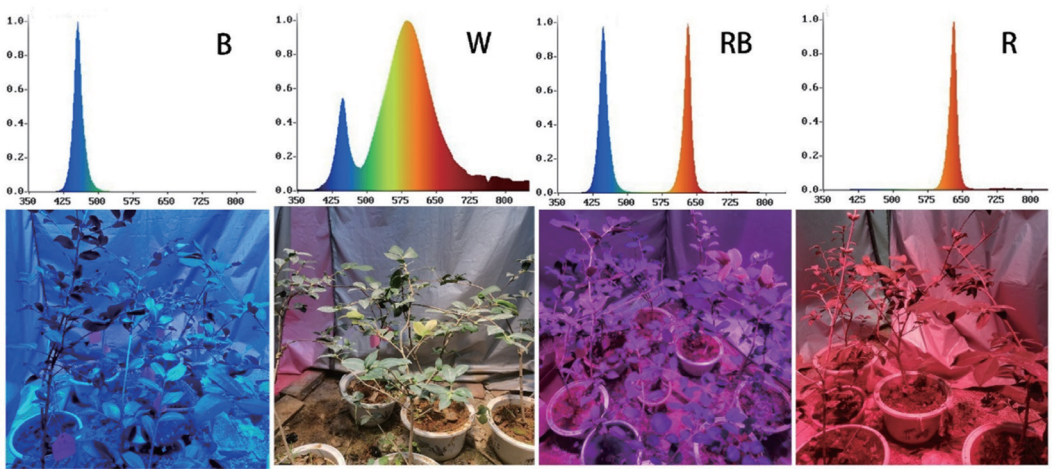

Fig. 1. Light spectra of different treatment qualities. B, blue light; W, white light; RB, combination of red and blue light; R, red light.

were replicated three times. The height of the LED light source was adjusted to ensure a photosynthetic photon flux density of 150 ± 10 μmol m^{-2} s^{-1} for each treatment. LED lights in the greenhouse provided 12 h of light per day (08:00 to 20:00), for 1 yr, and the internal greenhouse temperature was maintained at 25 ± 1 °C.

Growth parameter analysis

Growth parameters were measured when buds began to grow in March 2021. Five *C. oleifera* seedlings were randomly selected from each treatment, and the number of buds and maximum number of clumps of buds were recorded. Clumps of buds comprise a complex number of buds at the top of a single branch. The length from the base of the current shoot to the tip was measured using vernier calipers and repeated every 10 d for 50 d.

Photosynthetic parameter analysis

Photosynthetic parameters were measured using the LI-6400XT Portable Photosynthesis System (LI-COR, Lincoln, USA). In each treatment, 3 leaves from the 2nd to the 3rd youngest and middle and upper mature leaves of a new shoot were measured. The age difference between young leaves and mature leaves was half a year. Measurements included photosynthetic gas exchange parameters, a light response curve, and chlorophyll fluorescence parameters. Photosynthetic gas exchange parameters were measured from 09:00 to 11:00 on a sunny day with the CO_2 concentration set to 400 ppm, and illumination from a preset light (in a transparent leaf chamber). Light irradiation with 800 μmol m^{-2} s^{-1} was used for 30 min before the light response curve measurement. The light intensity gradients were set to 1500, 1200, 1000, 800, 600, 400, 200, 150, 100, 75, 50, 25, and 0 μmol m^{-2} s^{-1}. The light response curves were fit using a modified model of a right-angled hyperbola (Ye 2007). Apparent quantum efficiency, maximum net photosynthetic rate ($P_{n\text{-}max}$), light compensation point (LCP), dark respiration rate (R_d) and saturated light intensity (L_{sat}) were obtained by Photosynthesis Calculation software (JGSU, Jinggangshan, China). Chlorophyll fluorescence parameters were determined by changing the fluorescent leaf chamber. Plants to be tested were exposed to sunlight for 30 min, and then the maximum photochemical efficiency of photosynthetic system II (Φ_{PSII}) and the electron transport rate (ETR) were measured. Plants were placed in a dark environment and the minimal fluorescence (F_o) and maximal fluorescence (F_m) were measured after the plant leaves had completely adapted to the darkness. The light source was then turned on to activate the same leaves, and the steady state fluorescence (F_s), maximal fluorescence (F_m'), and minimal fluorescence (F_o') were measured after activation was complete. Photochemical quenching (q_P), non-photochemical quenching (q_N), and the maximum photochemical quantum yield (F_v/F_m) were calculated using the following equations (Genty et al. 1989; Bilger and Björkman 1990; Van and Snel 1990):

$$F_v/F_m = \frac{F_m - F_o}{F_m}, \quad (1)$$

$$q_P = \frac{F'_m - F_s}{F'_m - F'_o}, \quad (2)$$

$$q_N = \frac{F_m - F'_m}{F'_m}. \quad (3)$$

Stomatal observations

In July 2021, 3 young and 3 mature leaves were randomly selected from each treatment. The leaves were cleaned with water, and when the surface of a leaf was free of moisture, clear nail varnish was applied to both sides of the main veins on the dorsal surface of the leaf and allowed to air dry.

Transparent tape was applied over the dried nail varnish on the dorsal leaf surface and was subsequently peeled off to obtain epidermal prints. The transparent tape was then affixed to a slide and observed under a microscope at a magnification of 20×. The images obtained were analyzed using ImageJ 1.8 software (NIH, Bethesda, USA). The number of stomata was calculated for each treatment at 5 random sites of 300 × 300 μm in the image. The stomatal number of the 1-mm^2 blade was calculated in proportion. The sizes of 10 randomly selected stomata were measured at each inspection site.

Leaf anatomical features

Three mature leaves were collected for each treatment, and the middle section of the leaf was fixed with a formalin aceto-alcohol solution and preserved in 70% alcohol. This was followed by paraffin sectioning using the following steps: dehydration, transparency, wax immersion, embedding, sectioning, dewaxing, staining, and sealing. Images were obtained using a microscope, and thicknesses of the leaf, palisade tissues, sponge tissues, and epidermis were determined using ImageJ software.

Chlorophyll content

Chlorophyll was extracted using a mixture of acetone and ethanol (acetone:ethanol = 2:1) (Dunn et al. 2004). Three mature leaves were randomly selected for each treatment, and the main leaf veins were removed and cut into fine threads. Then, 0.2000 g of leaves was weighed and added to 20 mL of the mixture, and the extraction was repeated three times. Absorbance values were measured at 645 and 663 nm, and the chlorophyll content was calculated using Arnon's formula (Arnon 1949):

$$C_a=12.71A_{663}-2.59A_{645}, \quad (4)$$

$$C_b=22.88A_{645}-4.67A_{663}, \quad (5)$$

$$C_{(a+b)}=C_a+C_b=20.29A_{645}+8.04A_{663}, \quad (6)$$

$$C_{(x,c)}=(1000A_{470}-3.27C_a-104C_b)/229, \quad (7)$$

$$Sample\ Pigment\ content=C*V/1000F_w; \quad (8)$$

where A_{663} and A_{645} are absorbance values at the corresponding wavelengths; V is the total volume of extracts (ml); F_w is the fresh weight of the leaves (g); C_a, C_b, $C_{x,c}$, and C_{a+b} are chlorophyll *a*, chlorophyll *b*, carotenoids, and total chlorophyll concentrations (mg/L), respectively; and *C* is the pigment content of the test solution.

Leaf nitrogen and phosphorus contents

To determine the nitrogen and phosphorus contents of leaves using the digestion method, 10–15 mature *C. oleifera* leaves were randomly taken from each treatment, dried, and then ground into a powder. Two grams of the powder was digested with sulfuric acid, and diluted and filtered after digestion. Total nitrogen and phosphorus contents of the leaves were determined using an intermittent analyzer. Each treatment was replicated 3 times.

Statistical analysis

All data were subjected to a one-way analysis of variance (ANOVA) using IBM SPSS vers. 26 software (SPSS, Armonk, USA). Figures were prepared using Graphpad Prism 8 (Graphpad, San Diego, USA) and ImageJ 1.8 software.

RESULTS

Growth parameter analysis

Treatment B produced the highest number of buds per plant, which was strikingly higher than that of the W and R treatments, but did not significantly differ from that of the RB treatment (Table 1). The highest number of clumped buds was observed in the B treatment group. Terminal shoot lengths of the B and RB treatments were considerably greater than that of treatment W, and that of treatment R was the shortest. There was no marked difference between the B and W treatments at 10 to 40 d. After 40 d, treatment W entered a stasis period, while treatment B was still rapidly growing. Our results indicated that red light had a certain inhibitory effect on the growth of terminal shoots of *C. oleifera*. The shoot length of treatment RB was significantly higher than those of treatments B and W at 20 d, indicating that shoots entered a rapid growth period earlier under RB treatment. In contrast, blue light and mixed red and blue light were beneficial for the elongation of current shoots of *C. oleifera*, while blue light promoted bud formation.

Photosynthetic parameters analysis

The net photosynthetic rate of leaves was the highest under treatment B, while the net photosynthetic rate of mature leaves under treatment RB was slightly lower than that under treatment B, but did not drastically differ (Fig. 2A). The stomatal conductance of young leaves under treatment RB was the highest and was significantly higher than those of the other treatments. Mature leaf stomatal conductance was the highest under treatment B but did not considerably differ from that under RB treatment (Fig. 2B). The intercellular carbon dioxide concentration of treatment B was significantly higher than that of treatment W, and they were similar among mature leaves (Fig. 2C). The highest transpiration rate of mature leaves under treatment B was markedly higher than those of the other treatments (Fig. 2D). The net photosynthetic rate, stomatal conductance, and transpiration rate were drastically lower under treatment R than under treatment W. Φ_{PSII} and q_P values of mature leaves under treatment B were slightly higher than those under RB treatment, but the difference was not significant (Fig. 2E, F). The q_N value of young leaves under treatment B was the lowest and was considerably lower than that of treatment RB, while q_N values of mature leaves were similar among all treatments (Fig. 2G). F_v/F_m values of young leaves were markedly higher under treatments B

Table 1. Effects of light quality on growth parameters of Camellia oleifera

Light quality	Number of buds per plant	Maximum number of cluster buds	10 d terminal shoot length (cm)	20 d terminal shoot length (cm)	30 d terminal shoot length (cm)	40 d terminal shoot length (cm)	50 d terminal shoot length (cm)
B	19.98±5.56a	6	22.36±3.72a	34.48±6.94b	57.72±10.01b	74.25±12.73a	82.05±18.43a
W	16.67±6.33b	4	22.27±3.56a	34.44±9.02b	55.83±7.39bc	65.93±13.14ab	68.51±13.16b
RB	18.15±5.12ab	5	25.84±6.83a	40.17±11.61a	62.84±14.73a	76.15±20.68a	85.64±21.02a
R	12.56±4.45c	4	18.8±4.84b	26.13±5.89c	47.78±7.30c	56.87±11.12b	59.27±16.09c

B, blue light; W, white light; RB, combination of red and blue light; R, red light. Note: Values are the mean±standard deviation. Different letters in a column indicate a significant difference ($p < 0.05$), based on a one-way ANOVA followed by the LSD test.

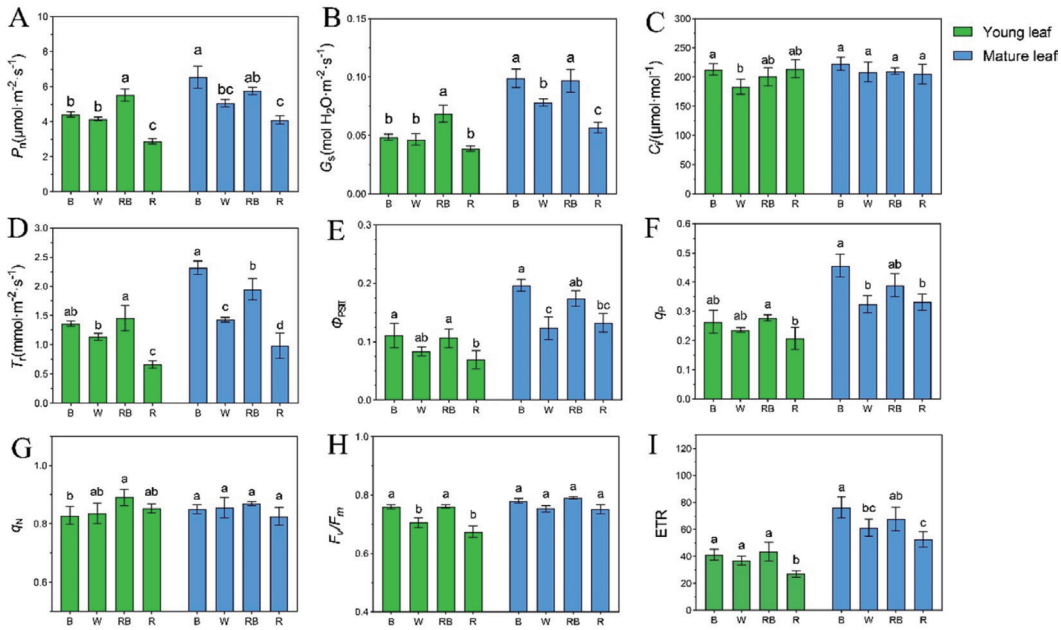

Fig. 2. Effects of light quality on photosynthetic parameters. A-D. Photosynthetic gas exchange parameters. E-I. Chlorophyll fluorescence parameters. P_n, net photosynthetic rate; G_s, stomatal conductance; C_i, intercellular CO_2 concentration; T_r, transpiration rate; Φ_{PSII}, photochemical quantum yield; q_P, photochemical quenching; F_v/F_m, maximum photochemical quantum yield; q_N, non-photochemical quenching; ETR, electron transport rate. Different letters indicate a significant difference ($p < 0.05$), based on a one-way ANOVA followed by the LSD test.

and RB than those under treatments W and R, and the differences among treatments were smaller in mature leaves (Fig. 2H). ETR values of young leaves were slightly higher under treatment RB than those under treatment B, whereas ETR values of mature leaves were higher under treatment B than those under treatment RB; none of them significantly differed (Fig. 2I). Φ_{PSII}, q_P, F_v/F_m, and ETR values were drastically smaller under treatment R than those under treatments B and RB.

In young leaves, RB treatment had the highest apparent quantum efficiency, but it did not markedly differ from treatments B and W. In mature leaves, treatment B had the highest apparent quantum efficiency (Table 2). The $P_{n\text{-}max}$ of mature leaves in treatment B was the largest, reaching 9.11 μmol m^{-2} s^{-1}. The maximum net photosynthetic rate of young leaves under treatment RB was significantly higher than those under other treatments. The saturated light intensity of treatment W was the highest in young leaves, and that of treatment B was the highest in mature leaves. The LCP was the largest in treatment R and the smallest in treatment W. The maximum net photosynthetic rate, minimum apparent quantum transport efficiency, R_d, and L_{sat} of mature and young leaves were the lowest under treatment R.

According to a comprehensive analysis of index values, the photosynthetic capacity of mature leaves under treatment B was slightly higher than that under RB treatment, but the difference was not significant. The

Table 2. Light response curve characteristic parameters

	Young leaf					Mature leaf				
	Apparent quantum efficiency	$P_{n\text{-}max}$ (μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$)	LCP (μmol photon $\cdot m^{-2} \cdot s^{-1}$)	R_d (μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$)	L_{sat} (μmol photon $\cdot m^{-2} \cdot s^{-1}$)	Apparent quantum efficiency	$P_{n\text{-}max}$ (μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$)	LCP (μmol·photon $m^{-2} \cdot s^{-1}$)	R_d (μmol·CO_2 $m^{-2} \cdot s^{-1}$)	L_{sat} (μmol photon $\cdot m^{-2} \cdot s^{-1}$)
B	0.077±0.01b	6.2±0.3b	10.5±0.1b	0.90±0.19a	730.4±7.6c	0.104±0.008a	9.1±0.4a	9.8±0.6a	0.75±0.17a	1462.5±21.2a
W	0.082±0.004a	5.9±0.3b	7.6±1.5c	0.58±0.03bc	938.8±8.2a	0.084±0.007b	7.5±0.4b	7.3±0.2c	0.57±0.09b	1229.1±13.5b
RB	0.084±0.004a	7.2±0.3a	10.3±0.6b	0.79±0.07ab	795.3±11.3b	0.083±0.003b	8.7±0.2a	8.5±0.9b	0.72±0.03a	1368.2±18.3a
R	0.031±0.003c	3.3±0.3c	14.7±1.0a	0.46±0.07c	698.7±5.8c	0.037±0.004c	5.8±0.3c	10.8±1.2a	0.38±0.10c	868±9.8c

B, blue light; W, white light; RB, combination of red and blue light; R, red light. Note: Values are the mean±standard deviation. $P_{n\text{-}max}$, maximum net photosynthesis rate; LCP, light compensation point; R_d, dark respiration rate; L_{sat}, saturated light intensity. Different letters in a column indicate a significant difference ($p < 0.05$), based on a one-way ANOVA followed by the LSD test.

photosynthetic capacity of young leaves under treatment RB was stronger than those under the other treatments. The photosynthetic capacity of *C. oleifera* leaves was inhibited under treatment R.

Stomatal observations

Treatment B had the most developed mature leaf stomata, whereas treatment RB had the densest stomata. The R treatment group had the smallest stomatal area, and the lowest stomatal conductivity (Fig. 3). The density of stomata did not drastically change during leaf maturation in the B and W treatment groups, but the area of individual stomata increased. Individual stomatal areas in the RB and R treatment groups varied less but considerably differed in density (Table 3). Results indicated that blue light caused the stomatal area of *C. oleifera* to increase, while red light increased stomata density. The lower stomatal conductance under red light was related to the smaller area of individual stomata.

Leaf structure analysis

Leaves of *C. oleifera* were the thickest

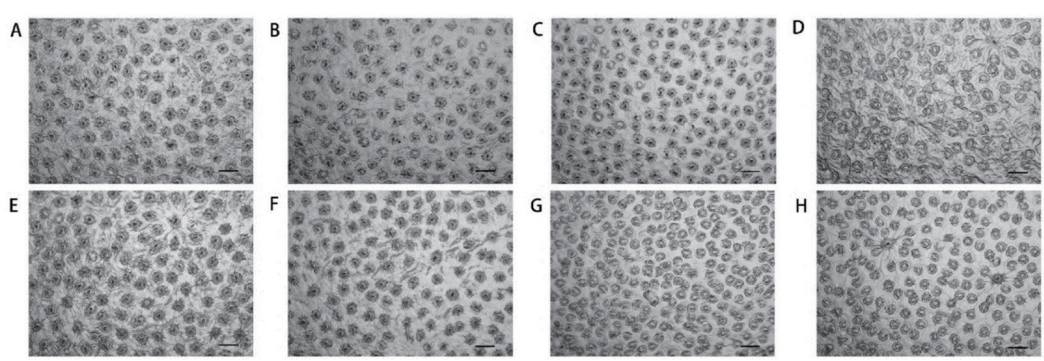

Fig. 3. Stomatal growth under various light treatments. Photographs were taken at 10× magnification. A. Blue light young leaf. B. White light young leaf. C. Red and blue mixed light young leaf. D. Red light young leaf. E. Blue light mature leaf. F. White light mature leaf. G. Red and blue mixed light mature leaf. H. Red light mature leaf. Scale bar = 50 μm.

under RB and B treatments (Table 4), followed by those under treatment R, whereas the leaves were the thinnest under treatment W. Both upper and lower epidermal thicknesses of the leaf blade showed the following trend: RB > B > W > R. Palisade mesophyll and spongy mesophyll thicknesses were considerably lower under W and R treatments than those under the other treatments, with there was little difference in palisade mesophyll thicknesses between the W and R treatments. However, greater spongy tissue thickness was recorded under treatment R compared to that under treatment W. The thickness of the palisade mesophyll in treatment B was less than that in treatment RB. In contrast, the thickness of the spongy mesophyll was greater under treatment B than that under treatment RB. As a result, there was no difference in the thickness of the leaves between the 2 treatments. Leaves of *C. oleifera* in the B and RB treatment groups had obvious layers of palisade and spongy tissues (Fig. 4), whereas the delineation between palisade and spongy tissues under treatments W and R was not as clear, and palisade cells were shorter. Results showed that white and red lights were not conducive to the formation of palisade and spongy tissues in *C. oleifera* leaves, while blue light and red and blue mixed lights were relatively favorable for leaf growth.

Table 3. Effects of light spectral quality on stomatal characteristics

	Young leaf stomatal density (no. per 1 mm^2)	Mature leaf stomatal density (no. per 1 mm^2)	Single stomatal area of young leaves (μm^2)	Single stomatal area of mature leaves (μm^2)
B	222±22b	256±33c	803±102ab	1003±117a
W	219±14b	222±33c	748±86bc	848±95b
RB	361±38a	433±33a	846±105a	851±91b
R	241±14b	333±33b	656±85c	614±46c

B, blue light; W, white light; RB, combination of red and blue light; R, red light. Note: Values are the mean±standard deviation. Different letters in a column indicate a significant difference ($p < 0.05$), based on a one-way ANOVA followed by the LSD test.

Table 4. Leaf anatomical structure of Camellia oleifera under different light qualities

Treatment	Thickness of upper epidermis (μm)	Thickness of lower epidermis (μm)	Thickness of palisade parenchyma (μm)	Thickness of spongy parenchyma (μm)	Thickness of blade (μm)
B	15.71±0.29ab	12.76±0.76ab	116.29±7.14a	219.71±8.86a	364.86±12.71a
W	14.48±0.76bc	12.00±1.14b	49.07±4.07b	124.71±5c	209.71±9.14c
RB	16.86±0.57a	13.90±0.48a	128.07±8.21a	210.43±7.57a	376.57±14.57a
R	13.90±1.33c	11.05±0.95c	47.02±4.02b	171.43±6.86b	261.37±9.49b

B, blue light; W, white light; RB, combination of red and blue light; R, red light. Note: Values are the mean±standard deviation. Different letters in a column indicate a significant difference ($p < 0.05$), based on a one-way ANOVA followed by the LSD test.

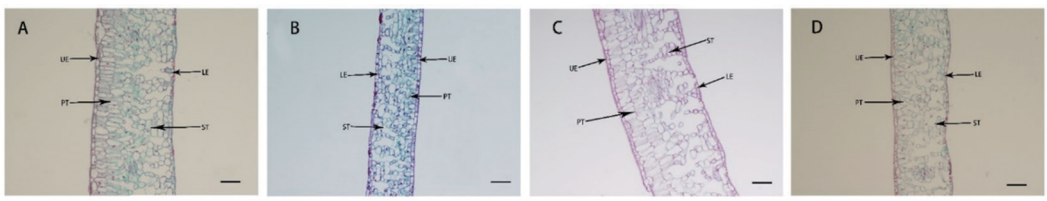

Fig. 4. Leaf anatomical structures of *Camellia oleifera* under different light qualities. Photographs were taken at 20× magnification. A. Blue light (B). B. White light (W). C. Red and blue mixed light (RB). D. Red light (R). UE, upper epidermis; LE, lower epidermis; PT, palisade mesophyll tissue; ST, spongy mesophyll tissue. Scale bar = 50 μm.

Photosynthetic pigment content analysis

The RB treatment group had the highest total chlorophyll content, while those of the W and R treatment groups did not significantly differ. The total chlorophyll content under treatment B was slightly lower than that under other treatments, with little difference in chlorophyll *a* contents among the W, RB, and R treatments. Treatment RB had the highest chlorophyll *b* content at 1.54 mg/g, which was considerably higher than those in the other treatment groups, whereas there were no major differences among the other treatments (Table 5). Carotenoid content under treatment R was significantly lower than those under other treatments. Chlorophyll *a*/*b* contents were markedly lower under treatment RB than those under the other treatments. Results showed that blue light had a greater inhibitory effect on chlorophyll *a* formation and red light had a greater inhibitory effect on carotenoid formation than other treatments, while the combination of red and blue light favored the formation of chlorophyll *b*.

Leaf nitrogen and phosphorus contents

N contents of *C. oleifera* leaves under all treatments did not significantly differ (Table 6). Different light qualities affected the phosphorus content of *C. oleifera* leaves; the highest phosphorus content of leaves under treatment B reached 5.01 mg/g on average, whereas the lowest phosphorus content of leaves under treatment W was only 4.01 mg/g. The phosphorus content of leaves under treatment B did not markedly differ from those

Table 5. Effects of light quality on chlorophyll content

	Chlorophyll *a* (mg/g FW)	Chlorophyll *b* (mg/g FW)	Total chlorophyll (mg/g FW)	Carotenoids (mg/g FW)	Chlorophyll *a*/*b*
B	1.91±0.03b	1.22±0.06b	3.13±0.06c	0.23±0.02a	1.57±0.05b
W	2.11±0.05a	1.19±0.05b	3.30±0.05b	0.20±0.01a	1.77±0.01a
RB	2.14±0.04a	1.54±0.05a	3.68±0.04a	0.22±0.02a	1.39±0.04c
R	2.10±0.08a	1.22±0.05b	3.32±0.05b	0.13±0.01b	1.72±0.08a

B, blue light; W, white light; RB, combination of red and blue light; R, red light; FW, fresh weight. Note: Values are the mean±standard deviation. Different letters in a column indicate a significant difference ($p < 0.05$), based on a one-way ANOVA followed by the LSD test.

Table 6. Effects of light quality on nitrogen (N) and phosphorus (P) contents

	B	W	RB	R
N (mg/g DW)	21.66±0.63a	22.14±0.57a	21.88±0.36a	22.51±0.28a
P (mg/g DW)	5.00±0.58a	4.01±0.38b	4.65±0.43ab	4.82±0.23a

B, blue light; W, white light; RB, combination of red and blue light; R, red light; DW, dried weight. Note: Values are the mean±standard deviation. Different letters in a row indicate a significant difference ($p < 0.05$), based on a one-way ANOVA followed by the LSD test.

of leaves under the RB and R treatments, but was much higher than that under treatment W. Results showed that the light quality had little effect on the nitrogen content of *C. oleifera* leaves, and blue and red light could increase the phosphorus content.

DISCUSSION

This study investigated the effects of light quality on the growth and development capacity of *C. oleifera* by subjecting it to different light qualities. The causes of this effect were investigated by measuring the structural anatomy and physiological indicators of the leaves.

In this experiment, blue light and red-blue mixed light promoted the growth and development of *C. oleifera*, while pure red light inhibited it. This effect was achieved by affecting the photosynthetic capacity and physiological structure. Light quality can affect photosynthesis by affecting the activity of the light system and the efficiency of electron transfer (Miao et al. 2016). Blue light may enhance the light utilization efficiency and photosynthetic capacity of *C. oleifera* leaves by improving photosystem activity and the efficiency of electron transfer. Red light decreases these parameters and therefore inhibits the photosynthetic capacity of leaves.

The photosynthetic efficiency and respiration rate of leaves determine the accumulation rate of nutrients. Light quality can control bud production and growth by affecting the distribution of nutrients and the response of photoreceptors. This study found that blue light irradiation increased the number of buds of *C. oleifera* seedlings. Bud formation is a key stage of plant growth and development (Leduc et al. 2012). Buds can develop into flowers or branches, which has important impacts on the flowering and fruiting of *C. oleifera*. Blue light can increase the number of buds by cryptochromes, and *CRY2* overexpression can increase the number of branches (Giliberto et al. 2005). Shoot growth length was greater under blue light and red-blue light, and least under pure red light, which was reported in many plants (Heo et al. 2002; Fukuda et al. 2016). This may be related to plant hormones, as red light can promote the synthesis of indoleacetic acid (IAA) (Liu et al. 2011), blue light can increase the activity of IAA oxidase to reduce the IAA content (Mei et al. 2013). The inhibitory effect of pure red light on shoot growth may be due to the synthesis of excessive IAA.

Light quality can regulate stomatal development through the cryptochrome-photosensitive pigment signaling system (Kang et al. 2009). Blue light can induce an increase in stomatal conductance by increasing the stomatal area (Ballard et al. 2019). Red light can specifically induce an increase in the density of stomata, while adding blue light can

increase this trend. The stomatal conductance in red light was markedly lower than that in the control group, and the lack of blue light might lead to stomatal closure. In this study, palisade tissue cell walls of *C. oleifera* leaves were regular and obvious under blue light, while they were irregular under red light. Light quality regulates leaf anatomy through gene expressions. Gene expression levels of actin, dynein, and tubulin in *C. oleifera* under blue light were significantly higher than those under white light and red light, and these proteins are involved in cell wall formation (Song et al. 2020). These highly expressed proteins may contribute to the development of palisade tissues under blue light. Palisade tissues contain numerous chloroplasts, and thicker palisade tissues in leaves are more conducive to photosynthesis.

The present study showed that treatment RB significantly increased the chlorophyll *b* content, and treatment B decreased the chlorophyll *a* content of oilseed tea leaves. The carotenoid content was considerably lower under red light than under other treatments. This is a manifestation of a plant's adaptation to the environment. A lack of red light reduced the content of chlorophyll *a*, which absorbs mainly violet and red light (Nürnberg et al. 2018), and the lack of blue light reduced the content of carotenoids, which would assist in the absorption of blue light energy (Hashimoto et al. 2018). The phosphorus contents of *C. oleifera* leaves under red and blue light were significantly higher than that under white light. Studies found that both red and blue light can promote the absorption of phosphorus by plant roots (Dong et al. 2022). Phosphorus can affect leaf photosynthesis through the organic phosphorus cycle and enzyme activity, and the leaf photosynthetic rate is usually positively correlated with the leaf phosphorus content (Tarryn et al. 2007; Richardson 2009). In this study, The higher phosphorus content under red light indicated that phosphorus was not a limiting factor of photosynthesis in *C. oleifera* leaves under red light.

CONCLUSIONS

Under blue light, the photosynthetic capacity of *C. oleifera* leaves was the strongest, and the plants could produce more buds, which was most beneficial to the growth and development of *C. oleifera*. Blue light can be used as an auxiliary light source for growing and strengthening seedlings.

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LITERATURE CITED

Arena C, Tsonev T, Doneva D, De MV, Michelozzi M, Brunetti C, et al. 2016. The effect of light quality on growth, photosynthesis, leaf anatomy and volatile isoprenoids of a monoterpene-emitting herbaceous species (*Solanum lycopersicum* L.) and an isoprene-emitting tree (*Platanus orientalis* L.). Environ Exp Bot 130:122-32.

Arnon DI. 1949. Copper enzymes in isolated chloroplasts, polyphenoloxidase in Beta vulgaris. Plant Physiol 24:1-15.

Ballard T, Peak D, Mott K. 2019. Blue and red light effects on stomatal oscillations. Funct Plant Biol 46(2):146-51.

Bilger W, Björkman O. 1990. Role of the xanthophylls cycle in photoprotection elu-

cidated by measurements of light-induced absorbance changes, fluorescence and photosynthesis in *Hedera canariensis*. Photosynth Res 25:173-85.

Centofante AR. 2020. Light quality on the morphoanatomy and physiology of *Campomanesia pubescens* (DC.) O. Berg. seedlings. Sci Hortic 259:108765.

Dong SJ, Ge SB, Li L, He LQ, Fan FJ, Qi ZY, et al. 2022. Effects of supplemental lighting on growth, root colonization by arbuscular mycorrhizal fungi and phosphorus uptake in pepper seedlings. Acta Hortic Sinica 49(08):1699-712. [in Chinese with English summary].

Dunn JL, Turnbull JD, Robinson SA. 2004. Comparison of solvent regimes for the extraction of photosynthetic pigments from leaves of higher plants. Funct Plant Biol 31(2):195-202.

Fang LZ, Ma ZY, Wang QB, Nian H, Ma QB, Huang QL, Mu YH. 2021. Plant growth and photosynthetic characteristics of soybean seedlings under different LED lighting quality conditions. J Plant Growth Regul 40(2):668-78.

Fukuda N, Ajima C, Yukawa T, Olsen JE. 2016. Antagonistic action of blue and red light on shoot elongation in *Petunia* depends on gibberellin, but the effects on flowering are not generally linked to gibberellin. Environ Exp Bot 121:102-11.

Gao C, Yang R, Yuan DY. 2017. Characteristics of developmental differences between fertile and aborted ovules in *Camellia oleifera*. J Am Soc Hortic Sci 142:330-6.

Genty B, Briantais JM, Baker NR. 1989. The relationship between quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. Biochim Biophys Acta 990:87-92.

Giliberto L, Perrotta G, Pallara P, Weller JL, Fraser PD, Bramley PM, et al. 2005. Manipulation of the blue light photoreceptor cryptochrome 2 in tomato affects vegetative development, flowering time, and fruit antioxidant content. Plant Physiol 137:199-208.

Hashimoto H, Uragami C, Yukihira N, Gardiner A, Cogdell R. 2018. Understanding/unravelling carotenoid excited singlet states. J R Soc Interface 15(141):20180026.

He CY, Zeng YL, Fu YZ, Wu JH, Liang Q. 2020. Light quality affects the proliferation of in vitro cultured plantlets of *Camellia oleifera* Huajin. Peerj 8:e10016.

Heyneke E, Fernie AR. 2018. Metabolic regulation of photosynthesis. Biochem Soc Trans 46(2):321-8.

Heo J, Lee C, Chakrabarty D, Paek K. 2002. Growth responses of marigold and salvia bedding plants as affected by monochromic or mixture radiation provided by a light-emitting diode (LED). Plant Growth Regul 38:225-30.

Kang CY, Lian HL, Wang FF, Huang JR, Yang HQ. 2009. Cryptochromes, phytochromes, and COP1 regulate light-controlled stomatal development in *Arabidopsis*. Plant Cell 21:2624-41.

Leduc N, Roman H, Barbier F, Péron T, Huché-Thélier L, Lothier J, et al. 2014. Light signaling in bud outgrowth and branching in plants. Plants (Basel) 3(2):223-50.

Li Y, Xin GF, Wei M, Shi QH, Yang FJ, Wang XF. 2017. Carbohydrate accumulation and sucrose metabolism responses in tomato seedling leaves when subjected to different light qualities. Sci Hortic 225:490-7.

Liu X, Cohen JD, Gardner G. 2011. Low-fluence red light increases the transport and biosynthesis of auxin. Plant Physiol 157(2):891-904.

Lv BS, Zhu JY, Kong XP, Ding ZJ. 2020. Light participates in the auxin-dependent regulation of plant growth. J Integr Plant Biol 63:819-22.

Mckown AD, Guy RD, Quamme LK. 2016. Impacts of bud set and lammas phenology on root: shoot biomass partitioning and carbon gain physiology in poplar. Trees 30(6):2131-41.

Miao YX, Wang XZ, Gao LH, Chen QY, Qu M. 2016. Blue light is more essential than red light for maintaining the activities of photosystem II and I and photosynthetic electron transport capacity in cucumber leaves. J Integr Agric 15(1):87-100.

Mei XL, Zhao Z, Chen XD, Lan J. 2013. Light quality regulation of growth and endogenous IAA metabolism of *Ganoderma lucidum* mycelium. China J Chin Mater Med 38(12):1887-92. [in Chinese with English summary].

Nürnberg DJ, Morton J, Santabarbara S, Telfer A, Joliot P, Antonaru LA, et al. 2018. Photochemistry beyond the red limit in chlorophyll f-containing photosystems. Science 360(6394):1210-3.

Richardson AE. 2009. Regulating the phosphorus nutrition of plants: molecular biology meeting agronomic needs. Plant Soil 322:17-24.

Shafiq I, Hussain S, Raza MA, Iqbal N, Ahsan AM, Raza A, et al. 2021. Crop photosynthetic response to light quality and light intensity. J Integr Agric 20(1):4-23.

Sims L, Pastor J, Lee T, Dewey B. 2012. Nitrogen, phosphorus and light effects on growth and allocation of biomass and nutrients in wild rice. Oecologia 170(1):65-76.

Song QQ, Chen SP, Wu YF, He YF, Feng JL, Yang ZJ, et al. 2020. Comparative transcriptome analyses of gene response to different light conditions of *Camellia oleifera* leaf using illumina and single-molecule real-time-based RNA-sequencing. Forests 11(1):91.

Tarryn LT, Charles RW, Mark AA. 2007. Novel mannose-sequestration technique reveals variation in subcellular orthophosphate pools do not explain the effects of phosphorus nutrition on photosynthesis in *Eucalyptus globulus* seedlings. New Phytol 176(4):849-61.

Van KO, Snel JFH. 1990. The use of chlorophyll fluorescence nomenclature in plant stress physiology. Photosynth Res 25:147-50.

Ye ZP. 2007. A new model for relationship between irradiance and the rate of photosynthesis in *Oryza sativa*. Photosynthetica 45:637-40.