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ORIGINAL PAPER

Response of photosynthetic pigments, gas exchange and chlorophyll fluorescence parameters to light quality in *Phoebe bournei* seedlings

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Abstract

To reveal responses of photosynthetic physiological characteristics in *Phoebe bournei* seedlings to different light qualities and provide a basis for light environment regulation in seedling cultivation and under-canopy regeneration, we analyzed the photosynthetic physiological characteristics of *P. bournei* seedlings under five types of light qualities (white, red, blue, green, red: blue = 1:1) with the same photosynthetic photon flux density of 100 ± 5 μmol·m^{-2}·s^{-1}. The results showed that blue light significantly promoted chlorophyll content, Rubisco, RCA and photosynthetic rate (*P*n), but water use efficiency (WUE) was reduced by blue light. The red light treatment exhibited the highest initial fluorescence (*F*o), but wasn't conducive to the accumulation of photosynthetic pigments and had the lowest maximum photochemical efficiency (*F*v/*F*m) and potential photochemical efficiency (*F*v/*F*o). The seedlings treated by green light showed the lowest *P*n, *T*r, WUE, rubisco, with the highest *F*v/*F*m and *F*v/*F*o. Red-blue light significantly increased WUE, photosynthetic electron transfer rate (ETR), actual photosynthetic efficiency Y(II), and quantum yield of regulated energy dissipation Y(NPQ) in PSII of *P. bournei* seedlings, with the second highest *Pn* across treatments. In conclusion, the effects of single light quality on photosynthetic characteristics of *P. bournei* seedlings exhibited both advantages and disadvantages. The combination of red and blue light, which integrated the advantages of single light quality, enhanced the photosynthetic performance and photoprotective ability of *P. bournei* seedlings. It promoted the energy conversion and utilization efficiency of PSII, resulting in the best carbon assimilation efficiency. Therefore, red-blue light promoted the growth and development of *Phoebe bournei* seedlings.

Keywords *Phoebe bournei* seedling · Light quality · Photosynthetic pigment · Gas exchange · Chlorophyll fluorescence

Abbreviations

Chl*a*	Chlorophyll a
Chl*b*	Chlorophyll b
*C*i	Intercellular CO_2 concentration
CK	Control treatment
ETR	Photosynthetic Electron Transfer Rate
*F*o	Initial fluorescence
*F*m	Maximum fluorescence
*F*v/*F*m	Maximum photochemical efficiency
*F*v/*F*o	Potential photochemical efficiency
*G*s	Stomatal conductance
J_{max}	Maximum electron transfer rate
NPQ	Non-photochemical quenching coefficient
PAR_{sat}	Saturated light intensity
*P*n	Photosynthetic rate
PSII	Photosystem II
*q*P	Photochemical quenching coefficient
RCA	Rubisco activase
Rubisco	Ribulose-1,5-bisphosphate carboxylase/oxygenase
*T*r	Transpiration rate
WUE	Water use efficiency
Y(NO)	Quantum yield of non-regulated energy dissipation
Y(NPQ)	Quantum yield of regulated energy dissipation
Y(II)	Actual photosynthetic efficiency
α	Initial slope

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Introduction

Light is the source of energy for plant photosynthesis, and the photomorphogenesis of plants is controlled by light quality (Fang et al. 2021). Plant photoreceptors and photosynthetic pigments jointly receive light signals, which regulate both stomatal movement and chloroplast structure, as well as photosynthetic pigments (Li et al. 2013). They can activate or inhibit a series of physiological responses in plants and control plant photomorphogenesis (Li et al. 2013). Various light qualities or wavelengths exert distinct biological effects on morphological structure, chemical composition, photosynthesis, organ growth, and plant development.

Many studies on the effect of light quality on plant photosynthetic characteristics have shown that controlling spectral composition can optimize plant quality and yield (Paradiso and Proietti 2022). It has been reported that red light (R) can regulate the development of photoreceptors and photosynthetic organs in some species, activate the photosynthetic process and regulate morphogenesis, thereby increasing photosynthetic products and promoting plant growth (Sb et al. 1995; Yu et al. 2017). However, some studies showed that red light itself was not suitable for cultivating seedlings. For instance, *Lactuca sativa*, *Boehmeria nivea*, and *Fragaria* × *ananassa* grown under red light exhibited lower photosynthetic capacity compared to tose cultivated under blue light (Johkan et al. 2012; Rehman et al. 2020; Yoshida et al. 2016). These results indicated that there are differences in the response of different plants to light quality. Light quality plays an important role in regulating the biosynthesis of photosynthesis-related pigments (Zhang et al. 2021). Blue light is very important for chloroplast development and photosynthesis (Hogewoning et al. 2010; Sb et al. 1995). The chlorophyll content, carotenoid content, and chlorophyll a/b ratio of increased under blue light, which increased stomatal conductance and intercellular CO_2 concentration through inducing stomatal opening (Hogewoning et al. 2010; Sb et al. 1995). High-intensity short-wave green (G) light can effectively activate the photosynthetic rate of *Lactuca sativa* leaves and significantly increase plant growth and net photosynthetic rate (Johkan et al. 2012). Green light plays a special role in regulating plant growth and metabolism, which can penetrate deeper foliage and understory plants, promoting plant growth by stimulating the carbon assimilation of plants below the plant canopy (Kim et al. 2004). Wang et al. (2015) showed that a single red or blue light could not meet the growth requirements of plants. A high ratio of red-blue light was beneficial to the growth of plants at the seedling stage (Wang et al. 2015). Blue light (425–490 nm) and red light (610–700 nm) have been identified as the optimal spectra for plant photosynthesis (Chang and Chang 2014). Red-blue light can increase the accumulation of nitrogen in leaves, which improves photosynthetic rate, light energy utilization and product quality by increasing leaf area and biomass, and promotes plant growth and development (Han et al. 2015; Ohashi-Kaneko et al. 2006). At present, there are few reports on the response mechanisms of woody seedlings to light quality, and more studies on crops (Riikonen 2021). Previous studies have shown that light quality can affect the nutrient content of both aboveground and underground parts of *Pinus koraiensis* seedlings (Wei et al. 2020). Red light promotes the growth of *Picea abies* seedlings (OuYang et al. 2021). Song et al. (2020) explored the effect of light quality on *Camellia oleifera* at the physiological and transcriptomic levels, and found that plants under blue light showed better growth. The importance of light quality for plant growth and its role as a pivotal signal in plant development are evident (Fu and Chin 1992; Zheng 1983).

Phoebe bournei (Hemsl.) Yang belongs to the family of Lauraceae, which is a precious tree species, and a shade tolerant species (Fu and Chin 1992; Zheng 1983). Because of its excellent timber and beautiful wood grain, it became a high-grade building material for the imperial palace in ancient China (Tang et al. 2020). *P. bournei* is naturally distributed in the subtropical climate zone with a warm and humid conditions (An et al. 2022). The wild resources of *P. bournei* have significantly depleted due to prolonged logging, exploitation, and utilization. In recent years, *P. bournei* plantation forestry has gradually increased, and the demand for seedlings has increased. In the investigation of *P. bournei* natural forests in the field, it was observed that there were significant differences in the number and growth of *P. bournei* seedlings in different understory light environments (Han et al. 2021), which might be caused by the heterogeneity of light intensity and light quality. Some studies with appropriate shade treatment increased the photorespiration of *P. bournei*, which can improve photosynthetic CO_2 assimilation by decreasing photorespiratory metabolites (Tang et al. 2020). The biomass, chlorophyll content and net photosynthetic rate of *P. bournei* increased significantly with increasing degree of shading (An et al. 2022). The rapid growth of *P. bournei* seedlings may be the result of accelerated expression of genes related to photosynthesis and chlorophyll, which enable plants to maintain high photosynthetic rates even under low light conditions (An et al. 2022). However, the effect of light quality on *P. bournei* seedlings was neglected. The spectral component received by *P. bournei* seedlings under the canopy will change due to the absorption, reflection and scattering of incident light by the upper layer of the forest canopy. While, it is unclear about how the light quality affects the photosynthetic physiological characteristics and growth of *P. bournei* seedlings.

Therefore, we designed a pot experiment with different types of light qualities to investigate the effects of light quality on photosynthetic pigments, gas exchange parameters, key photosynthetic enzyme activities and chlorophyll fluorescence characteristics of *P. bournei* seedlings. The objective was to reveal the response and adaptation of *P. bournei* seedlings to different light quality. Our research aims to provide a scientific basis for regulating seedling growth through artificial light supplementation.

Materials and methods

Experimental material and light treatments

P. bournei seedlings were grown in germination trays (seeds were collected from the same tree in Baili Village, Gangdu Town, Huishui County, Guizhou Province, China). Seedlings with similar growth (7.0 ± 0.85 cm in height; 1.20 ± 0.08 mm in diameter) were selected and transplanted into pots filled with a peat: perlite = 4:1 mixed matrix in May. Two seedlings were planted per pot, with each pot measuring 15.5 cm in diameter and 14 cm in height. After the seedlings have recovered, placed them in a light-light quality incubator (FH-740, Hipoint, Taiwan) with different light quality for culture experiments.

The light quality and light intensity were measured under *P. bournei* natural forest in Taijiang County, Guizhou Province, China, and the parameters of the photosynthetic photon flux density in incubator were set according to the data from the field environment. All light sources were provided by light-emitting diodes (LEDs). Four kinds of light quality treatments were set, namely red light (R, 660 nm), blue light (B, 450 nm), green light (G, 525 nm) and red-blue light BR (red light: blue light = 1:1). White light was used as a control (CK). Each treatment consisted of three replicates, with 12 seedlings per replicate. The parameters of the incubator were set as follows: photon flux density of 100 ± 5 μmol·m^{-2}·s^{-1}, relative humidity of 70% ± 5%, photoperiod of 14 h/10 h and temperatures of 28 °C ± 0.5 °C/20 °C ± 0.5 °C (day/night). The substrate was kept moist by watering it once every three days. Treatment was started on June 25, 2020 and lasted for 60d. At the end of the treatment, the fully expanded leaves with vigorous growth on the upper portion of the seedlings were selected for determination of the indices.

Measurement of chlorophyll content

Ethanol extraction method was used for determination of chlorophyll (Min et al. 2018). Fresh leaves of *P. bournei*, were picked, washed and dried, while the main veins were removed. 0.1 g of functional leaves were weighed and put into a scaled test tube and added into 10 ml 95% ethanol to extract for 48 h under dark conditions. After the leaves turned white, the absorbance of chlorophyll was measured by UV spectrophotometer at 665 nm, 649 nm and 470 nm. According to the specific absorption coefficient of chlorophyll in 95% ethanol solution, the chlorophyll content was calculated by following formula (Gao 2006).

$$Chla\left(mg \cdot g^{-1}\right) = \frac{(13.95 \times A665 - 6.88 \times A649) \times V}{1000 \times W}$$

$$Chlb\left(mg \cdot g^{-1}\right) = \frac{(24.96 \times A649 - 7.32 \times A665) \times V}{1000 \times W}$$

$$Car\left(mg \cdot g^{-1}\right) = \frac{(1000 \times A470 - 2.05 \times Chla - 114.8 \times Chlb) \times V}{245 \times 1000 \times W}$$

$$\mathrm{Chl}a/b = \mathrm{Chl}a/b$$

where V (ml) is the total volume of ethanol extract, and W (g) is the weight of fresh leaves.

Measurement of gas exchange parameters

In mid-September 2020, the gas exchange parameters of *P. bournei* seedlings were determined from 9 to 10 a.m. on a sunny day by portable open infrared gas exchange analyzer system (LI-6800; LI-Cor Inc., Lincoln, NE, USA) and a red and blue light source leaf chamber (6800–02). Firstly, the leaves of *P. bournei* seedlings were induced for 30 min in the leaf chamber with the optical quantum flux density of 1000 μmol·m^{-2}·s^{-1}, CO_2 concentration of 400 μmol·mol^{-1} and temperature of 28℃. The parameters including net photosynthetic rate (*P*n), stomatal conductance (*G*s), intercellular CO_2 concentration (*C*i) and transpiration rate (*T*r) were obtained, and the leaf water use efficiency of signal leaf was calculated as: (WUE) = *P*n /*T*r.

Measurement of chlorophyll fluorescence parameters

The chlorophyll fluorescence parameters were determined using a portable multichannel continuous fluorescence monitor (Monitoring-PAM, Heinz Walz GmbH, Effeltrich, Germany). The leaves were determined after 1 h of dark adaptation. The measured indices include initial fluorescence (*F*o) and maximum fluorescence (*F*m). The variable fluorescence *F*v (*F*v = *F*m-*F*o), maximum photochemical efficiency of PSII (*F*v/ *F*m), and potential photochemical efficiency of PSII (*F*v /*F*o) were calculated based on *F*o and *F*m.

Meanwhile, the rapid light response curves of *P. bournei* leaves under different light quality treatments were measured by a fluorescence monitor, and the photosynthetically active radiation (PAR) gradients were set to 0, 90, 125, 190, 285,

420, 625, 820, and 1150 μmol·m^{-2}·s^{-1}. According to the method proposed by Ye et al. (2010), the initial slope (α), maximum electron transfer rate (J_{max}) and saturated light intensity (PAR_{sat}) were fitted with an online model developed by Ye (http://photosynthetic.sinaapp.com/).

Measurement of photosynthetic key enzyme activities

The Rubisco and RCA contents of *P. bournei* leaves were measured by ELISA kits (Shanghai Keshun Biotechnology Co., LTD., Shanghai, China). The Rubisco and RCA contents of seedlings were determined by the double antibody sandwich assay method. First, the functional leaves of uniform size and at the same node position from each treatment were collected and rapidly frozen in liquid nitrogen, stored at − 80 °C. Second, leaf tissues (1 g) were ground into powder in liquid nitrogen and homogenized in 9 mL precooled enzyme extract buffer. The homogenate was centrifuged in a microcentrifuge at 8000 rpm at 4 °C for 30 min. The supernatant and Reagents 1 through 5 were then added in turn to a 96–well plate according to the instructions at room temperature (25 °C). Finally, absorbance (OD value) was measured at 450 nm using a microplate reader (Tecan Austria GmbH; Untersbergstr, 1A, A-5082 Grodig; Austria), and the enzyme content for each treatment was calculated based on the corresponding standard curve (Shuya et al. 2022; Li et al. 2020).

Microtiter plate wells were coated with purified Rubisco or RCA capture antibodies to prepare solid-phase antibodies. Then Rubisco or RCA was added to the coated micropores, and then combined with the HRP labeled detection antibody to form an antibody-antigen-enzyme-labeled antibody complex. After thorough washing, the substrate TMB was added for color development. The TMB was converted into blue under the catalysis of HRP enzyme and into the final yellow under the action of acid. The shade of the color is positively correlated with the Rubisco or RCA in the plant.

Statistical analysis

Experiments were performed in a comprehensively random design. Values presented are mean ± standard deviation (SD) of three replicates. Microsoft Excel (2010) was used to calculate the basic test data. All data were tested for normality and homogeneity of variance (Levene's test) before statistical analyses, and when necessary, were log-transformed. The data were analyzed using one-way analysis of variance (ANOVA), and mean values were compared using the Duncan's multiple range test ($p < 0.05$). Pearson correlation analysis was used to determine the correlation between photosynthetic parameters ($p < 0.05$). All statistical analyses were conducted using SPSS 26.0 for Windows. Origin 2021 software was used for chart drawing.

Results

Response of photosynthetic pigments to light quality in *P. bournei* seedlings

Different light quality treatments had different effects on photosynthetic pigments of *P. bournei* seedlings (Fig. 1), and the content of Chl*a* and Chl*b* differed significantly between treatments ($p < 0.05$). Under blue light, the contents of Chl*a*, Chl*b*, and Car in *P. bournei* seedling leaves reached their highest values, which were significantly higher than those under other light quality treatments ($p < 0.05$). Specifically, Chl*a*, Chl*b*, and Car increased by 9.58%, 19.42%, and 12.77%, respectively, compared with the control (CK). However, the Chl*a/b* was the lowest under the blue light, which was 8.52% lower than CK. The differences in content

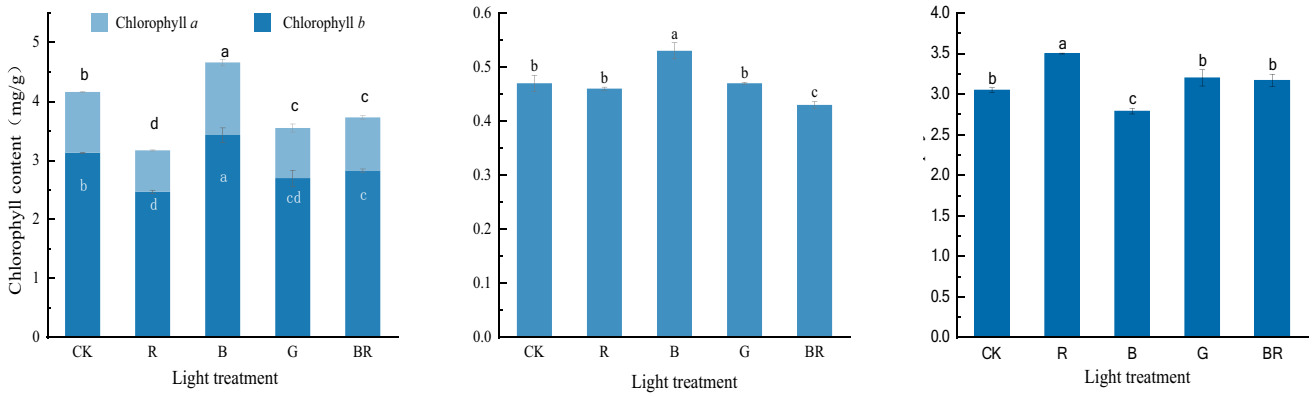

Fig. 1 Response of photosynthetic pigments to light quality in *P. bournei* seedlings. *CK* white light, *R* red light, *B* blue light, *G* green light, *BR* red-blue light (1:1). Vertical bars indicate standard error (n = 3). Different lowercase letters in the same column represent significant differences at $p < 0.05$ among treatments by the Duncan's multiple range test

of Chl*a* and Chl*b* between the green light and red-blue light treatments were not significant ($p > 0.05$). The contents of Chl*a* and Chl*b* of *P. bournei* seedling leaves under red light treatment were lower, but its Chl*a/b* was the highest, which was 1.15 times higher than that of CK g.

Response of photosynthetic characteristics to light quality in *P. bournei* seedlings

Gas exchange parameters

The results demonstrated that light quality had significant effects on gas exchange parameters of *P. bournei* seedlings (Table 1). The *P*n, *T*r and *G*s of leaves in *P. bournei* seedlings under blue light were significantly higher than those under other light treatments ($p < 0.05$), which were 1.47, 1.60 and 1.85 times of CK, respectively. Its *C*i was second only to the green light treatment, 10.26% higher than CK, and the WUE is only higher than that of the green light treatment. The *C*i of red-blue light treatment was the lowest, and there was no significant difference compared with CK and red light treatment ($p > 0.05$). The WUE of red-blue light treatment was 76.95% higher than that of green light treatment. The *P*n, *T*r and WUE of leaves under green light were lower than CK by 67.41%, 44.14% and 41.35%, respectively. However, its *C*i was significantly higher than that of the other light quality treatments, and was 22.46% higher than CK. The stomatal conductance of *P. bournei* leaves under red light was the lowest, only 50.86% of CK.

Content of photosynthetic enzymes

The Rubisco enzyme content of *P. bournei* leaves under blue light was the highest, but there was no significant difference among CK, green light and red-blue light treatments ($p > 0.05$) (Fig. 2). The content of Rubisco enzyme in red light was the lowest, and the Rubisco enzyme content in blue light was increased by 22.58% compared with that in red light. RCA content of different treatments was significantly different ($p < 0.05$), and the enzyme content in descending order was B > CK > BR > R > G. RCA of blue light treatment was increased by 11.67%, 80.61%, 122.89% and 55.37% compared with CK, red light, green light and red-blue light, respectively.

Response of chlorophyll fluorescence parameters to light quality in *P. bournei* seedlings

Chlorophyll fluorescence parameters

There were significant differences in fluorescence parameters of *P. bournei* seedlings under different light qualities ($p < 0.05$) (Table 2). The initial chlorophyll fluorescence

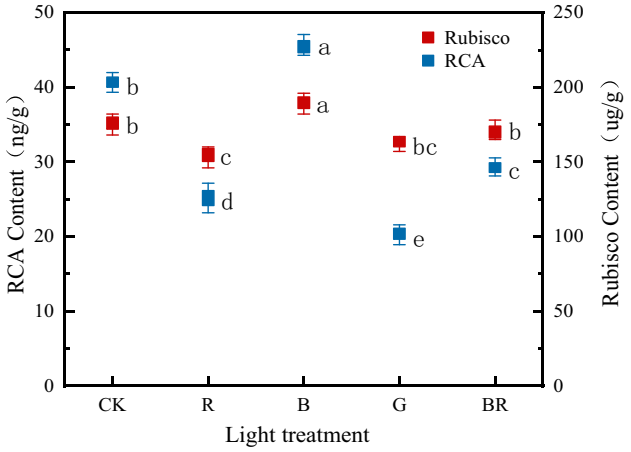

Fig. 2 Response of photosynthetic key enzymes content to light quality in *P. bournei* seedlings. *CK* white light, *R* red light, *B* blue light, *G* green light, *BR* red-blue light (1:1), *RCA* Rubisco activase, *Rubisco* Ribulose-1,5-bisphosphate carboxylase/oxygenase. Vertical bars indicate standard error (n = 3). Different lowercase letters in the same column represent significant differences at $p < 0.05$ among treatments by the Duncan's multiple range test

(*F*o) was R > CK > G > BR > B. The *F*o of red light treatment increased by 10.14% compared with CK, and increased by 55.09% compared with blue light treatment. The maximum fluorescence (*F*m) showed G > CK > BR > B > R. The maximum photochemical efficiency (*F*v/*F*m) and potential photochemical efficiency (*F*v/*F*o) of PSII were the highest under green light and the lowest under red light. There was no significant difference in *F*v/*F*o and *F*v/*F*m between red-blue light and blue light treatments ($p > 0.05$). The *F*m, *F*v/*F*m and *F*v/*F*o of *P. bournei* seedlings treated with green light increased by 80.57%, 16.79% and 137.45% compared with the lowest red light treatment, and increased by 3.2%, 2.21% and 8.35% compared with CK, respectively.

The increase in photosynthetically active radiation (PAR) led to a rapid decline in *q*P, followed by a gradual stabilization (Fig. 3). When PAR < 300 μmol·m^{-2}·s^{-1}, the *q*P of blue and red light treatments were higher. When PAR > 300 μmol·m^{-2}·s^{-1}, the *q*P of red-blue light treatment exceeded that of blue light treatment and was higher than that of other treatments. Under the same PAR condition, the *q*P of red light treatment decreased the fastest, and the *q*P of green light treatment was the lowest. This indicated that the PSII reaction center of *P. bournei* was more open and absorbed more light energy for photosynthesis under red-blue light. Non-photochemical quenching (NPQ) represents the dissipation of light energy absorbed by PSII that cannot be utilized for photosynthetic electron transport, manifested as heat dissipation. The trend in NPQ exhibited an inverse relationship with that of *q*P. With increasing PAR, NPQ initially increased and subsequently reached a plateau. When

Table 1 Response of gas exchange parameters to light quality in *P. bournei* seedlings

Treatment	*Pn* (μmol m^{-2} s^{-1})	*Gs* (mmol m^{-2} s^{-1})	*Ci* (μmol mol^{-1})	*Tr* (mmol m^{-2} s^{-1})	WUE (μmol/mmol)
CK	2.139 ± 0.015c	26.363 ± 0.051c	255.380 ± 0.864c	0.777 ± 0.001b	2.752 ± 0.018b
R	1.116 ± 0.020d	13.408 ± 0.021d	256.334 ± 2.091c	0.435 ± 0.001c	2.564 + 0.042c
B	3.145 ± 0.026a	48.640 ± 0.083a	281.579 ± 0.689b	1.240 ± 0.002a	2.537 ± 0.017c
G	0.697 ± 0.039e	14.822 ± 0.933d	312.732 ± 1.455a	0.434 ± 0.027c	1.614 ± 0.020d
BR	2.382 ± 0.010b	29.414 ± 0.040b	254.418 ± 0.698c	0.834 ± 0.001b	2.856 ± 0.015a

CK white light, *R* red light, *B* blue light, *G* green light, *BR* red-blue light (1:1), *Pn* Photosynthetic rate, *Gs* Stomatal conductance, *Ci* Intercellular CO_2 concentration, *Tr* Transpiration rate, *WUE* Water use efficiency. Different lowercase letters in the same column represent significant differences at $p < 0.05$ among treatments by the Duncan's multiple range test

Table 2 Response of basic chlorophyll fluorescence parameters to light quality in *P. bournei* seedlings

Treatment	*Fo*	*Fm*	*Fv*/*Fm*	*Fv*/*Fo*
CK	585.333 ± 1.202b	2554.000 ± 0.577b	0.769 ± 0.001c	3.353 ± 0.009c
R	644.667 ± 3.756a	1459.667 ± 2.906e	0.673 ± 0.001d	1.530 ± 0.006d
B	415.667 ± 2.603e	1880.333 ± 0.882d	0.779 ± 0.001b	3.520 ± 0.012b
G	570.000 ± 2.646c	2635.667 ± 3.180a	0.786 ± 0.001a	3.633 ± 0.015a
BR	463.333 ± 0.882d	2089.667 ± 0.882c	0.780 ± 0.002b	3.537 ± 0.009b

CK white light, *R* red light, *B* blue light, *G* green light, *BR* red-blue light (1:1), *Fo* Initial fluorescence, *Fm* Maximum fluorescence, *Fv*/*Fm* Maximum photochemical efficiency, *Fv*/*Fo* Potential photochemical efficiency. Different lowercase letters in the same column represent significant differences at $p < 0.05$ among treatments by the Duncan's multiple range test

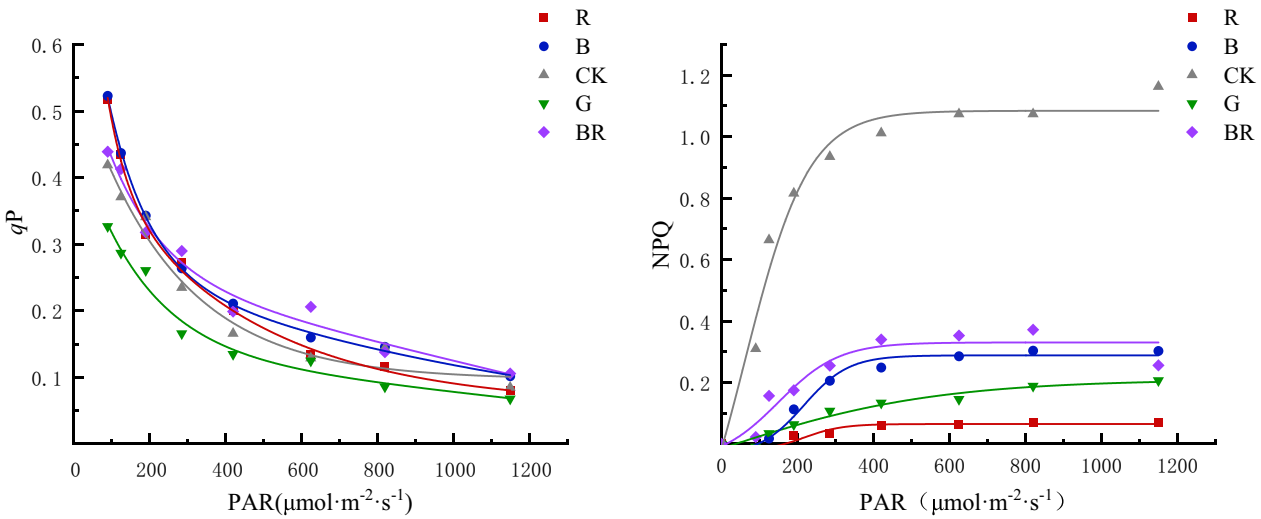

Fig. 3 Response of photochemical quenching coefficient (*q*P) and non-photochemical quenching coefficient (NPQ) to light quality in *P. bournei* seedlings. *CK* white light, *R* red light, *B* blue light, *G* green light, *BR* red-blue light (1:1), *NPQ* Non-photochemical quenching coefficient, *q*P Photochemical quenching coefficient

PAR < 400 μmol·m^{-2}·s^{-1}, NPQ increased almost linearly. When PAR was between 400 and 1100 μmol·m^{-2}·s^{-1}, the variation of NPQ gradual reached saturation, and the NPQ showed CK > BR > B > G > R. It exhibited that most of the light energy absorbed by leaves of CK could not be used for photosynthetic electron transfer, but dissipated in the form of heat. The NPQ of red and green light treatments were low, so the light protection ability was poor, which may be damaged by light.

Table 3 Response of photosynthetic parameters α, J_{max} and PAR_{sat} to light quality in *P. bournei* seedlings

Treatment	Initial slope(α)	J_{max}(μmol m^{-2} s^{-1})	PAR_{sat}(μmol m^{-2} s^{-1})
CK	0.075	26.85	1223.6
R	0.105	19.37	696.9
B	0.107	27.57	979.8
G	0.073	18.86	876.3
BR	0.103	32.57	1189.1

CK white light, *R* red light, *B* blue light, *G* green light, *BR* red-blue light (1:1), J_{max} Maximum electron transfer rate, PAR_{sat} Saturated light intensity, α Initial slope

The light response of chlorophyll fluorescence and energy partitioning

The simulation of the ETR-response curve revealed distinct trends among the various light quality treatments. With the increase of photosynthetically active radiation, the apparent electron transfer rate continued to increase, and finally tended to be stable and reached saturation (Fig. 4A). Within the range of 200–1200 μmol·m^{-2}·s^{-1} of PAR, the order of ETRs was BR > B > CK > R > G under identical conditions. The α values of CK and green light treatment were lower than those of red light, blue light and red-blue light (Table 3). The PAR_{sat} values of CK and red-blue light treatment were higher, which was 75.58% and

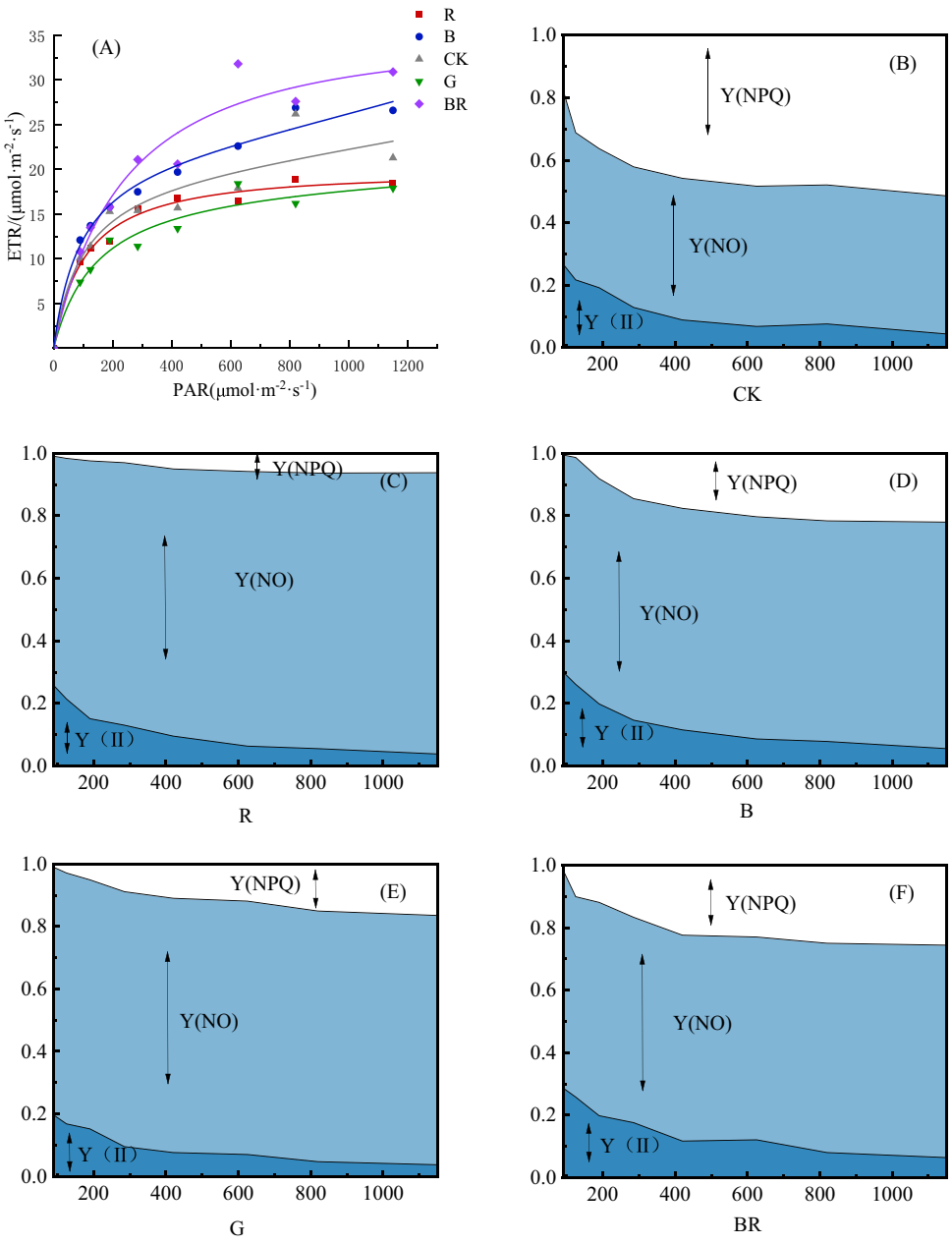

Fig. 4 **A** ETR-response curve of *P. bournei* seedlings under different light qualities. **B–F** The response of PSII actual photosynthetic efficiency Y(II) 、Quantum yield of regulated energy dissipation Y(NPQ) and Quantum yield of non-regulated energy dissipation Y(NO) to light quality in *P. bournei* seedlings. *CK* white light, *R* red light, *B* blue light, *G* green light, *BR* red-blue light (1:1), *ETR* Photosynthetic Electron Transfer Rate, *Y(NO)* Quantum yield of non-regulated energy dissipation, *Y(NPQ)* Quantum yield of regulated energy dissipation, *Y(II)* Actual photosynthetic efficiency

70.63% higher than that of red light. The J_{max} of red-blue light treatment was the highest, 21.30% higher than CK. Red-blue light significantly increased ETR and α rapidly. Under different light qualities, the energy distribution of PSII in the leaves of *P.bournei* seedlings changed with PAR (Fig. 4B-F). As the PAR increased, the Y(II) initially decreased and then reached a plateau, while the Y(NPQ) exhibited an initial increase followed by stabilization. The Y(NO) fluctuated in accordance with the values of Y(II) and Y(NPQ). In energy allocation, the proportion of Y(II) in CK was slightly lower than that in blue and red-blue light treatments, while Y(NPQ) was the highest. This indicated that the leaves accept excess light intensity under white light, but white light treatment can dissipate excess light energy into heat energy to protect themselves, and most of the energy is used for light protection. Compared with other treatments, Y(II) and Y(NPQ) were lower in green and red light treatments, while Y(NO) was higher. These results indicated that the regulation mechanism of photochemical energy conversion and protection (such as heat dissipation) of leaves under red and green light were insufficient to fully dissipate the light energy absorbed by seedlings. The seedlings were exposed to more light than they can receive and may be damaged by light. Y(II) was higher under blue and red-blue light treatments. However, compared with blue light treatment, red-blue light treatment had higher Y(NPQ) and lower Y(NO), so as to achieve the best photosynthetic efficiency.

Correlation analysis

The correlation analysis (Fig. 5) showed that Rubisco in the leaves of *P. bournei* seedlings was extremely significantly correlated with Chl*a* and Chl*b* ($p < 0.001$), and was significantly correlated with *P*n, *T*r and RCA ($p < 0.05$). The RCA was significantly correlated with *P*n, *T*r, Chl*a* and Chl*b* ($p < 0.05$). The *T*r was significantly correlated with *P*n ($p < 0.01$), and was significantly correlated with Chl*a* and Chl*b* ($p < 0.05$). The Chl*a* was significantly correlated with Chl*b* ($p < 0.001$). The *F*v/*F*m was significantly correlated with *F*v/*F*o ($p < 0.001$). A significant negative correlation was observed between *G*s and *F*o, as well as between *C*i and WUE ($p < 0.05$). However, no significant correlation was found between Car and the other measured parameters.

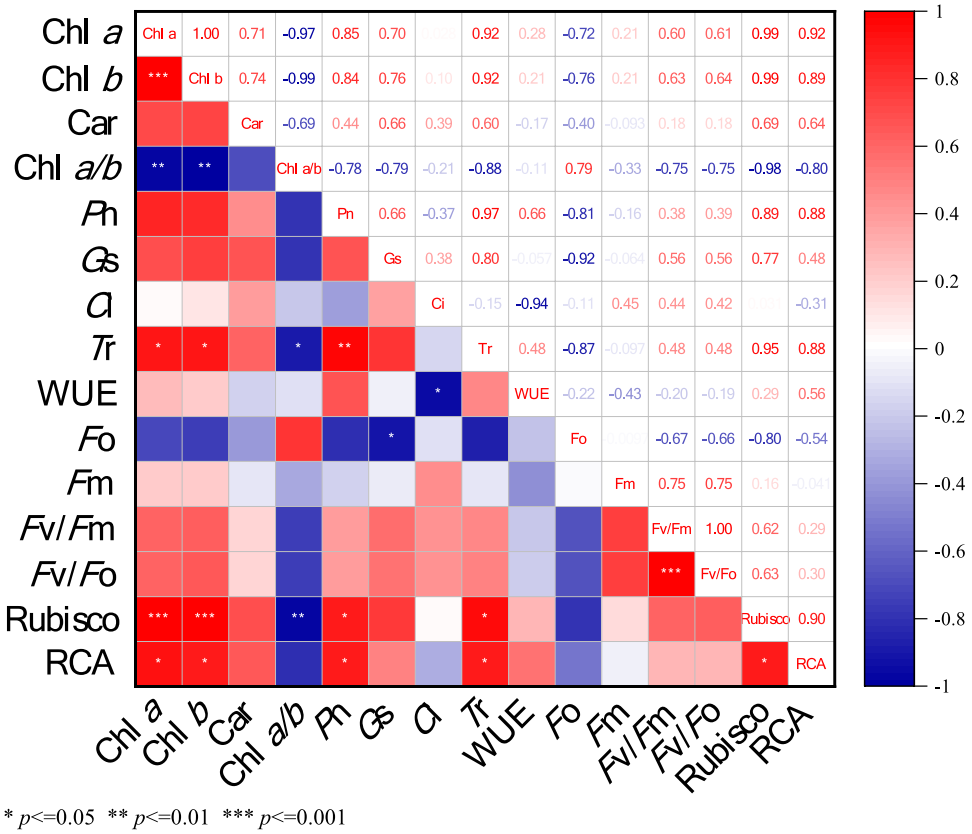

Fig. 5 Correlation analysis between photosynthetic pigment, gas exchange and chlorophyll fluorescence parameters of *P. bournei* seedlings. Chl*a* Chlorophyll a, Chl*b* Chlorophyll b, *P*n Photosynthetic rate, *G*s Stomatal conductance, *C*i Intercellular CO_2 concentration, *T*r Transpiration rate, *WUE* Water use efficiency, *RCA* Rubisco activase content, *Rubisco* Ribulose-1,5-bisphosphate carboxylase/oxygenase content, *F*o Initial fluorescence, *F*m Maximum fluorescence, *F*v/*F*m Maximum photochemical efficiency, *F*v/*F*o Potential photochemical efficiency

Discussion

Relationship between light quality and photosynthetic pigments

Plants sense light signals through photoreceptors (Galvao and Fankhauser 2015). Among these photoreceptors, phytochromes are responsible for perceiving red light, while cryptochromes and certain phytochromes perceive blue light. Additionally, some phytochromes are also capable of perceiving green light (Galvao and Fankhauser 2015). Upon perceiving changes in the light quality of the environment, the photoreceptor initiates a cascade of cellular responses, governing its own metabolic processes, energy regulation, and exerting control over plant photomorphogenesis, photosynthetic pigments, enzyme synthesis (Taiz and Zeiger 2010). Previous studies have suggested that spectra including blue wavelengths enhance the production of photosynthetic pigments (Dieleman et al. 2019; hogewoning et al. 2010). Blue light is required for chlorophyll synthesis and chloroplast formation in higher plants (Taiz and Zeiger 2010). Blue light stimulates the production of chlorophyll and carotenoids through cryptochrome, which is conducive to the accumulation of pigments (Fan et al. 2013a, 2013b; Sood et al. 2005; Tanaka et al. 1998; Weller et al. 2001). It can reverse the inhibitory response induced by red light, while red light is not conducive to pigment accumulation (Fan et al. 2013a, 2013b; Sood et al. 2005; Tanaka et al. 1998; Weller et al. 2001). However, in the study of *Boehmeria nivea* and *Lactuca sativa*, it was found that the content of chlorophyll and carotenoids increased in red light treatment, suggesting that red light was more conducive to the synthesis of photosynthetic pigments than blue light (Rehman et al. 2020; Shimizu et al. 2011). In this study, the contents of chlorophyll components and carotenoids in the leaves of *P. bournei* seedlings under blue light treatment was the highest, while that under red light treatment was lower. The chlorophyll content of red-blue light treatment was significantly increased because blue light reversed the inhibitory response induced by red light. Chlorophyll a is a component of both photosynthetic reaction centers and the light-harvesting antennae, while chlorophyll b is synthesized from chlorophyll a and is only located in the antenna complexes (Fang et al. 2021). Chlorophyll b has a strong absorption around 450 nm, which is a region of light that chlorophyll a cannot effectively absorb. It has a spectral absorption region compensation effect and can capture a wider range of light (Tanaka and Tanaka 2011). Chlorophyll b is also required for the stabilization of the major of the structure of light-harvesting complex (LHC) proteins (Tanaka and Tanaka 2011). The peak wavelengths of chlorophyll a and b absorption spectra differ by about 20 nm (Kume et al. 2018; Xu et al. 2020). Chlorophyll a/b is an important determinant of the light absorption efficiency of photosynthesis (i.e. antenna size), which can reflect the changes of the optical system (Kume et al. 2018; Xu et al. 2020). The results of this study showed that the chlorophyll a/b value was lowest under blue light. Blue light may promote the conversion of chlorophyll a to chlorophyll b to a large extent, and the light energy absorption capacity is was improved. Then the chlorophyll a/b value was positively correlated with the red/blue ratio. This contradicts previous studies investigating the effects of light quality on *Fragaria* × *ananassa*, *Lycopersicon esculentum* and *Dendrobium huoshanense*. Their results showed that the chlorophyll a/b value increased under blue light (Johkan et al. 2010; XUKai et al. 2004; Yang et al. 2018). The observed disparity between our findings and previous results could be attributed to the divergent light requirements among plant species, with each species exhibiting specific responses to varying light qualities. Then, variations in photosynthetic pigment content may arise from the differential light perception capabilities of different plant photoreceptors.

Relationship between light quality and photosynthetic characteristics

Rubisco is an enzyme that catalyzes the assimilation of carbon dioxide in photosynthesis and is the most abundant leaf protein on earth (Carmo-Silva et al. 2015). As the core of plant productivity, it is the only enzyme that can support the net assimilation of carbon and increase biomass (Carmo-Silva et al. 2015). Rubisco activase (RCA), a catalytic chaperone of Rubisco, which can regulate the activity of Rubisco enzyme and is one of the key regulatory mechanisms of light on carbon fixation (Nagarajan and Gill 2018). Like other AAA + ATPases, RCA uses the energy from ATP hydrolysis to remodel the conformation of its target protein, Rubisco (Carmo-Silva and Salvucci 2013; Nagarajan and Gill 2018; Snider et al. 2008). Studies by Lorimer (2003) and Vicente et al. (2011) showed that the content of chlorophyll and Rubisco was often considered as indicators of the light capture and Calvin cycle ability of leaves. The rate of photosynthesis and biomass accumulation largely depended on the content and activity of Rubisco (Lorimer 2003; Vicente et al. 2011). In the study of *Lycopersicon esculentum*, Izzo et al. (2020) found that the Rubisco content and photochemical efficiency of seedlings under red light were the lowest, while the heat dissipation was the highest, and the photosynthetic capacity decreased. In addition, most studies showed that blue light significantly increased *G*s and Rubisco activity, up-regulated the transcription levels of genes encoding Calvin cycle enzymes and Rubisco small subunits, and

significantly improved the photosynthetic efficiency of genes encoding which mediated regulation of Rubisco enzyme activity (RCA) (Hung et al. 2022; Kuno and Furuya 2000; Li et al. 2021b; Su et al. 2014; Tepperman et al. 2001; Wang et al. 2009). The biosynthesis of Rubisco and the expression of RCA increased in seedlings grown under blue light (Hung et al. 2022; Kuno and Furuya 2000; Li et al. 2021b; Su et al. 2014; Tepperman et al. 2001; Wang et al. 2009). In this study, Rubisco and RCA in the leaves of *P.bournei* seedlings were significantly correlated with Chl*a*, Chl*b*, *P*n and *T*r. The indicators exhibited the highest values under blue light, lower values under green and red light, and the red-blue light treatment showed values comparable to CK. These findings were consistent with previous studies on cabbage and cucumber (Hu et al. 2017; Su et al. 2014). Studies conducted by Hu et al. (2017) and Su et al. (2014) indicated that alterations in *P*n were consistently accompanied by changes in *G*s, Rubisco synthesis, as well as the transcription and expression of key genes involved in the Calvin cycle. Among them, blue light was conducive to photosynthesis of seedlings. The content of Rubisco was the highest in the seedlings induced by blue light, which was more important for the function of photosynthetic organs than red light. Therefore, we speculated that blue light mainly acted on the cryptochrome in the leaves of *P.bournei* seedlings, promoted the synthesis of more photosynthetic pigments, and significantly increased the content of Rubisco enzyme and RCA protein. Then it enhanced the ability of Calvin cycle, catalytic carbon dioxide assimilation. Therefore, blue light increased the *P*n and *T*r of leaves, and the photosynthetic performance of *P. bournei* seedlings was improved.

Blue light is an environmental signal mediated by its specific photoreceptors that induces stomatal and chloroplast movement and development (Terashima et al. 2016; Inoue and Kinoshita 2017). Higher stomatal conductance can promote higher net photosynthetic rate, but at the cost of more water loss (Matthews et al. 2017; Naumburg and Ellsworth 2000). In this study, *C*i was significantly negatively correlated with WUE. Blue light promoted *C*i and *G*s of *P.bournei* seedlings, resulting in the highest *P*n and *T*r, while the WUE of leaves was lower under blue light. It indicated that blue light enhanced the ability of carbon dioxide in and out of *P. bournei* leaves, thus improved the photosynthetic rate, but also caused more water loss, which confirmed the previous conclusions. Under red and blue light treatment, *C*i concentration was the lowest and WUE was the highest, while *P*n and *T*r were second only to blue light treatment. The results showed that the seedlings used carbon dioxide and water more effectively and harvested a good photosynthetic rate under red-blue light. Therefore, we speculated that the leaves of *P.bournei* seedlings treated with red-blue light had higher photosynthetic potential and photosynthetic utilization efficiency, as well as stronger photosynthetic utilization ability, which was consistent with the results of Fu et al. (2016) and Han et al. (2015).

Photoprotection mechanism and light energy distribution model

Chlorophyll fluorescence refers to the re-emission of light by chlorophyll molecules from the excited state to the non-excited state, which is used to regulate the photosynthetic energy conversion of plant leaves (Maxwell and Johnson 2000). The study of Lysenko et al. (2020) showed that the absorbed light energy was redistributed from the upper thin mesophyll layer to the lower cell layer throughout the entire leaf. The green light sensing system can harmoniously regulate plant growth and development with red and blue light sensors (Folta and Maruhnich 2007). Blue/red light is mainly absorbed by the upper layer cells, while the lower layer cells by low radiation to emit low fluorescence and have little influence on the upper layer saturation (Lysenko et al. 2020). The upper layer cells exhibit weak absorption of green light, while the lower layer consists of thick tissues that predominantly absorb green light and emit fluorescence (Smith et al. 2017; Nishio 2000). The fluorescence can enter the upper cells upward, fully affecting their saturation (Smith et al. 2017; Nishio 2000). Therefore, green light can better induce chlorophyll fluorescence kinetic behavior, thus significantly increases *F*v/*F*m and *F*v/*F*o. Kalaji et al. (2017) and Li et al. (2021b) found that *F*'v /*F*'m and ΦPSII levels were higher in plants under red-blue light, then leaf openness and electron transfer efficiency of PSII were improved. Therefore, more electrons can be absorbed, captured and transferred, which improves the efficiency of excitation energy captured by PSII reaction center and enhances the resistance of plants to photoinhibition (Li et al. 2021b). In this study, *F*m, *F*v/*F*m and *F*v/*F*o were the highest under green light treatment, followed by *F*v/*F*m and *F*v/*F*o under red-blue light treatment, which was consistent with previous research conclusions. Therefore, this further indicated that the efficiency of capturing excitation energy of the PSII reaction center in leaves treated with green light was higher than that of red-blue light, that is, the inherent light energy conversion ability and potential light energy conversion efficiency were high, and green light may play a special role in regulating photosynthetic characteristics of plants (Li et al. 2021a; Su et al. 2014). Under the same PAR condition, the *q*P of red-blue light treatment was the highest, indicating that the PSII reaction center was more open. In the PAR-NPQ fitting curve, the NPQ of CK was significantly higher than that of other light quality treatments, followed by red-blue and blue light treatments, while red and green light treatments were lower. It showed that the light energy absorbed by the leaves under white light was mostly dissipated in the form of heat. However, red light

and green light treatments have poor photoprotection ability, which may be damaged by light. Red-blue light and blue light treatments' leaves have strong heat dissipation capacity. Even if the light intensity received by the plant is excessive, they can also protect themselves by dissipating excess light energy into heat.

The results showed that in the PAR-ETR fitting curve, the J_{max} was the highest under red-blue light, while PARsat ranked second only to white light. Furthermore, the initial slope (α) was also observed to be higher. Red-blue light can rapidly increase ETR and α, enhance PSII antenna pigment absorption and light energy utilization and ETR activity, improve the efficiency of light energy utilization of photosynthetic organs. This confirmed the previous speculation that red-blue light treatment has a stronger ability to utilize photosynthetic. The light energy absorbed by the PSII reaction center is used for photosynthesis, regulatory energy dissipation and non-regulatory energy dissipation, respectively. $Y(II) + Y(NPQ) + Y(NO) = 1$. Y(II) represents the actual photosynthetic efficiency; that is, the actual efficiency of light energy conversion. The actual photosynthetic efficiency of blue light and red-blue light treatments was higher. The difference was that the blue light treatment allocated a larger proportion of light energy to Y(NO), while the red-blue light treatment allocated more light energy to Y(NPQ). It showed that although *P. bournei* received excess light energy under red-blue light, it could still avoid photoinhibition and damage to the system through regulated energy consumption (Wang et al. 2022). The blue light treatment had a higher Y(NO), indicating that the energy regulation mechanism of blue light treatment was to obtain as significant Y(II) as possible by maintaining a higher Y(NO) ratio, so as to adapt to changes of light intensity. Therefore, the light damage of blue light treatment consumed more energy, and the light energy utilization efficiency was low. Red-blue light treatment achieved the best photosynthetic efficiency, heat dissipation and light protection ability was also better.

Conclusion

The impacts of varying light qualities on photosynthetic pigment and its proportion, activities of photosynthetic key enzymes, gas exchange parameters and chlorophyll fluorescence parameters in *P. bournei* seedlings were significant different. The blue light significantly promoted the photosynthetic pigments, activities of photosynthetic key enzyme and photosynthetic rate (*P*n), while the water use efficiency (WUE) was lower. Green light treatment had the maximum potential photochemical efficiency (*F*v/*F*o) and maximum photochemical efficiency (*F*v/*F*m). Red light treatment inhibited the photosynthetic performance of *P. bournei*. The combination of red light and blue light was very important for the growth and development of *P. bournei* seedlings, and the proper ratio of red, blue and green light can better meet the needs of the seedlings for light resources. Therefore, we will further explore the appropriate ratio of red, blue and green light of *P. bournei* during the stage of seedlings in the future, so as to accurately regulate the spectral demand of the growth and development of *P. bournei* seedlings, which is conducive to the efficient cultivation of high-quality *P. bournei* seedlings.

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Author contributions All authors contributed to the study conception and design. WXL and JNQ designed the experiment, JNQ, NRX and CXY coordinated the experiment. NRX performed statistical analysis and formulated the manuscript. NRX, SSC and WXL revised and improved the manuscript.

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Data availability The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding authors.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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