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Different LED light qualities alter tomato plant growth and performance of two herbivores

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With 3 figures

Abstract: Bottom-up effects are major ecological forces driving crop-arthropod pest interactions in agroecosystems. Light is an important resource for plants, alters plant growth traits and trade-off their defensive ability through the bottom-up effects. In this study, we measured the effects of red (R), blue (B), red-blue (RB) and white (W, control) light on the growth traits of tomato plants and their defensive ability against whitefly *Bemisia tabaci* and western flower thrips *Frankliniella occidentalis*. Compared to the control, red, blue and red-blue light significantly affected the growth and defensive ability of tomato plants but to differing effects. Red light promoted plant height and stem diameter of tomato plants, inhibited photosynthetic traits and leaf thickness, which significantly decreased the fecundity of *B. tabaci* and *F. occidentalis*, and reduced the feeding and oviposition preference of *B. tabaci*. Blue light decreased the growth of tomato plants but increased photosynthetic parameters and leaf thickness and inhibited the fecundity of *B. tabaci*. Red-blue light was closest to the white control, slightly reducing growth of tomato plants but increasing leaf thickness and significantly decreasing the feeding and oviposition preference of *F. occidentalis*. These results indicated that red, blue and red-blue light had certain inhibitory effects on the performance of *B. tabaci* and *F. occidentalis*, and blue light also suppressed the growth and biomass accumulation of tomato plants. In conclusion, red and red-blue light reduced the performance of herbivores and optimally improve plant yield and quality in greenhouses.

Keywords: bottom-up effects; growth; defensive ability; *Bemisia tabaci*; *Frankliniella occidentalis*

1 Introduction

Plants exposed to various abiotic and biotic stress factors threatening biodiversity and ecosystem services in agroecosystems (Zhu 2016). These effects from the abiotic environment and/or organisms of lower trophic levels affect organisms of higher trophic levels through cascading effects, known as bottom-up effects of agroecosystems (Hunter & Price 1992). In agroecosystems, environmental factors, soil characteristics, crop resistance, crop diversity and other agricultural practice could trigger significant bottom-up effects and play an important role in driving crop-arthropod community dynamics (Han et al. 2022).

Light is a vital environmental factor and energy source for plants that profoundly influences plant growth and development throughout the life cycle of plants (De Wit et al. 2016; Lazzarin et al. 2021). Light quality, light intensity and photoperiod all play an important role to plants, but the effect of light quality is particularly important (Kusuma et al. 2020; Lazzarin et al. 2021). Plants have several classes of photoreceptors, all receiving different wavelengths of light from UV-B to far-red (FR, 700~800 nm). In solar radiation, only visible light (400–700 nm) is effective for plant photosynthesis, especially red (R, 600~700 nm) and blue (B, 400~500 nm) light (Li et al. 2021). Red and blue regions are mainly absorbed by plants via photosynthetic pigments, sensed by the phytochromes and three classes of blue photoreceptors including cryptochromes, phototropins, and members of the zeitlupe family, respectively, directly regulating photomorphogenesis and plant growth (Liu et al. 2021; Kong et al. 2021). Red and blue light qualities are therefore essential for normal growth and development of plants.

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The progress and use of light-emitting diodes (LEDs) has a significant enhancement of horticultural crop growth and development, largely due to their ability to manipulate the spectral composition of supplementary light (Bantis et al. 2018; Kusuma et al. 2020). The effects of different wavelengths of light on plant growth, development, photoreceptors and downstream responses, coupled with that on crop yield and quality, have been extensively studied (De Wit et al. 2016; Bantis et al. 2018). Compared with white (W) light or red-blue light (RB), monochromatic light generally has a negative effect on growth, development and physiological traits of plants (Liu et al. 2021). Red light generally improves plant height, increases leaf area and reduces leaf thickness and photosynthetic capacity (Izzo et al. 2020; Kong et al. 2021). In contrast, blue light inhibits plant height, promotes photosynthesis and leaf thickness, and induces stomatal opening and photosynthetic pigment accumulation (Kong et al. 2021; Chen et al. 2024). In addition, most reports have confirmed that red-blue light was an effective spectrum for healthy growth of plants and has been recommended as the preferred spectrum for agricultural production to improve crop yield and quality (Izzo et al. 2020; Li et al. 2021; Yousef et al. 2021).

However, these reports typically focus on commodity indicators such as yield and quality, but lack attention to effect light quality on plant defenses. Based on the trade-off of growth-defense, the use of different LED lights promotes plant growth while also affects plant defense against pathogens and herbivores through the bottom-up effects (Ballaré 2014; Zust & Agrawal 2017; Han et al. 2022). Recently, Meijer et al. (2022) reported that a low R: FR ratio of light, also known as shade avoidance syndrome (SAS), significantly increased the performance of *Manduca sexta, Tetranychus urticae, Myzus persicae*, and *Trialeurodes vaporariorum* feeding on tomato plants. Similarly, low ratio R: FR light stimulated the growth of *Arabidopsis thaliana*, but reduced resistance against *Spodoptera littoralis* and *Botrytis cinerea* (Fernandez-Milmanda et al. 2020). However, attention is typically only focused on the effect of invisible far-red light on herbivores or pathogens and there is a lack of exploration of the effects of how visible light, such as red and blue light, mediates plant-herbivore interactions and herbivore performance. Recent studies have shown that red light promoted the accumulation of salicylic acid (SA) by activating key biosynthesis genes of SA in melon and pepper respectively, and thus improved the resistance against powdery mildew and *Phytophthora capsica* (Wang et al. 2023; Yang et al. 2023). Therefore, it is necessary to evaluate the effects of visible light quality on plant defense, especially against herbivores. This will provide better assistance for pest control and promote optimal application of artificial lights in greenhouse crop production.

Tomato, *Solanum lycopersicum* L, a popular and important fruit and vegetable, is a crop widely distributed all over the world. At present, tomato is cultivated in China throughout the year and is also one of the horticultural crops with critical use of lighting technology (Kong et al. 2021). Two important pests on tomato plants, tobacco whitefly *Bemisia tabaci* and western flower thrips *Frankliniella occidentalis* (Di et al. 2022), were therefore selected to explore the effect of different light qualities on tomato plant growth and the performance of these two herbivores.

In this study, we investigated the effects of different LED light qualities on tomato plant growth traits and trade-off of the defensive ability. Under laboratory conditions, we measured the effects of red, blue, red-blue and white (control) light (following Li et al. 2021; Kong et al. 2021) on growth, biomass, leaf anatomy structure, photosynthetic traits and photosynthetic products of tomato plants. In addition, we evaluated the effect of different light qualities on the performance of *B. tabaci* and *F. occidentalis* through the bottom-up effects of tomato plants (Han et al. 2015, 2022). This study aimed to further understand the collaborative effects of different LED light qualities on plant growth and defense, considering both the yield and defensive ability of plants and providing additional supporting data for the application of artificial light in agriculture.

2 Materials and methods

2.1 Plant growing conditions and light quality treatments

The seeds of tomato, *Solanum lycopersicum* (cultivar, Qianxi), were sown in a 24-hole seed tray (36.5 × 23.0 × 5.5 cm) filled with growth medium of a mixture of peat soil, vermiculite and pearlite (3: 1: 1, V: V: V). Tomato seedlings were transplanted individually into a plastic flowerpot (8.0 × 8.0 × 10.0 cm) filled with the same growth medium at the two-true leaf stages, grown under controlled conditions in white light. After two days, all plants were randomly divided into four groups and grown under red light (R, peak wavelength at 655 nm), blue light (B, peak wavelength at 455 nm), red-blue light (RB, the ratio of photosynthetic photon flux density (PPFD), R: B = 1: 1) and white light (W), respectively. All lights were provided by LED at the same PPFD of 300 ± 20 μmol m^{-2} s^{-1} (Kedao, Huizhou, China). All plants were grown under controlled conditions at day/night temperature of (26 ± 2)/(18 ± 2) °C, relative humidity (RH) of 50 ± 5% and photoperiod of 16/8 h (day/night) in an insect-free artificial growth chamber. Tomato plants were used for the following experiments after 15 days of different LED quality treatments.

2.2 Insects rearing

Adults of *B. tabaci* were collected from tomato plants in the greenhouse of Beijing Noah Agricultural Science and Technology Co., LTD (Beijing, China). Adults and nymphs of *B. tabaci* were reared on cotton *Gossypium hirsutum* plants (cultivar, Zhongmian 49) in insect-rearing cages

(45 × 45 × 45 cm) made from metal frames and nylon yarn net (pore size: 150 μm) in a climate-controlled incubator (PGX-350D, Safe, Ningbo, China). The environmental conditions were controlled at 26 ± 1 °C, 60 ± 5% RH, 16: 8 h L: D photoperiod and a 30,000 Lux fluorescent light. To obtain whiteflies with the same age, new cotton plants were placed in the cages, the whiteflies were allowed to oviposit for 24 h, and the plants were kept in new cages for the insects to grow.

Frankliniella occidentalis adults were obtained from Institute of Plant Protection (IPP), Chinese Academy of Agricultural Sciences (CAAS, Haidian District, Beijing, China). These adults and nymphs were reared in a plastic box (24.8 × 18.0 × 9.0 cm) covered with a nylon yarn net (size: 20.0 × 14.0 cm; pore size: 150 μm). The plastic boxes were placed in a as described above climate-controlled incubator. Hyacinth bean *Lablab purpureus*, pods served as a food source and oviposition substrate, and were replaced every 2 days to obtain the same aged *F. occidentalis* from each rearing box.

2.3 Effects of different light qualities on tomato plants

Effects of different light qualities on growth of tomato plants

After 15 days of irradiation to different light qualities, six plants per treatment were randomly selected to assay for growth traits. Plant height was measured from the base of the main stem to the tip growth point of the stem, and stem diameter was measured in the internode nearest to the root by a vernier digital caliper. Dry weights (DW) of root, shoot and plant were measured by an analytical balance after drying at 105 °C for 30 min and 80 °C in an oven to a constant weight.

Effects of different light qualities on leaf anatomy structure of tomato plants

The small leaf positioned as the third leaf from the bottom of the plants was selected and positioned 10 mm away from the petiole for leaf anatomy measurements using a previously described method (Li et al. 2018) with some minor modifications. Pannoramic MIDI (3D Histech, Budapest, Hungary) was used for slice image acquisition. CaseViewer 2.43 (3D Histech, Budapest, Hungary) software was used to observe and analyze the anatomy structure and thickness of each tissue of tomato leaves. There were six biological replicates for each treatment. A total of six visual fields (3, 5 and 7 mm away from both sides of the main vein) were selected for each leaf, and the average value served as a biological replicate.

Effects of light qualities on gas exchange traits and photosynthetic pigments

The net photosynthetic rate (P_n), stomatal conductance (G_s), intercellular CO_2 concentration (C_i) and transpiration rate (T_r) of the third leaf from the bottom of the plants was measured using a photosynthesis system (LI-6400XT, LI-COR, Lincoln, NE, USA) during the daytime between 9:00~11:00. The conditions in the leaf chamber of the photosynthesis system included the PPFD of 300 μmol m^{-2} s^{-1}, CO_2 concentration of 400 μmol m^{-2} s^{-1}, leaf temperature of 26 °C, flow rate of 500 mL min^{-1}, and RH of 60%. Six plants per treatment were measured.

The chlorophyll (Chl a, Chl b, Chl a + b) and total carotenoid (Car) concentrations were measured with Plant Chlorophyll Content Assay Kit (BC0995, Solarbio, Beijing, China) and Plant Carotenoid Content Assay Kit (BC4335, Solarbio, Beijing, China) following the manufacturer's instructions, respectively. The third leaf from the bottom of six plants per treatment were measured.

Effects of different light qualities on photosynthetic products of tomato plants

The photosynthetic products of the third leaf from the bottom of tomato plants were measured. The soluble sugar, sucrose and starch content of tomato leaf evaluation was recorded using a Plant Soluble Sugar Content Assay Kit (BC0035, Solarbio, Beijing, China), Plant Sucrose Content Assay Kit (BC2465, Solarbio, Beijing, China) and Starch Content Assay Kit (BC0705, Solarbio, Beijing, China) following the manufacturer's protocols, respectively. Each treatment was replicated in six plants.

2.4 Performance of herbivores on tomato plants treated with light qualities

Survival rate

The same position of the third leaf from the bottom of the plants was fixed with a leaf cage (height = 3.0 cm, bottom diameter = 5.2 cm, and upper diameter = 6.6 cm). The leaf cage was made of a pudding cup, including the upper level covered with a nylon yarn net (diameter = 4.0 cm; pore size: 150 μm) with a small gap (diameter approximately 1 cm) on the side to allow the petiole to be wrapped with absorbent cotton and connected to the leaf cage. Twenty mated western flower thrips and female adult whiteflies (2~3 days after emergence) were carefully transferred to the leaf cage, respectively. After 3 days, the number of surviving adults was counted and recorded. There were fifteen replicates per treatment in this experiment.

Fecundity

Tomato plants and herbivores were treated as described above, except for the number of herbivores. Five mated female adults of the herbivores (*B. tabaci* and *F. occidentalis*, 2~3 days after emergence) were carefully inoculated into the leaf cage. After 3 days, adults of the two herbivores were removed from the leaf cage. The number of eggs of *B. tabaci* on treated leaves was recorded under a digital microscope (VHX-6000, Keyence, Japan), as a measure of the fecundity of *B. tabaci* (Di et al. 2022). The F1 nymph numbers of *F. occidentalis* per leaf cage were observed and recorded every day until there were no new hatched nymphs, as a measure of fecundity of *F. occidentalis* (Di et al. 2022). Each treatment was replicated fifteen plants.

Choice preference

To test the choice preference of herbivores (*B. tabaci* and *F. occidentalis*) for tomato plants treated with different light qualities, tomato plants from the white and red (W vs R), white and blue (W vs B) and white and red-blue (W vs RB) groups were used in paired choice tests using a choice device. The device consisted of a round plastic box (height 4 cm, bottom diameter 20 cm and upper diameter 24 cm) with an upper cover with two nylon net holes (4 × 4 cm) equal distance from each other and from the center and a gap (diameter approximately 1 cm) on both sides equal to the center, and a bottomless 1.5 mL centrifuge tube in the center of the upper cover to allow the herbivores to enter. The petiole of the third leaf from the bottom of the tomato plants from a pair (W vs R, W vs B, or W vs RB choice groups) was wrapped with absorbent cotton and placed in the gap on both sides of the device to connect the whole choice device. We then released 40 mated herbivores (*B. tabaci* or *F. occidentalis*), female adults aged 2~3 days after emergence, in the centrifuge tube of upper cover, from where they could move to any plant. The number of herbivores on each plant was observed and recorded after 24 h as a feeding preference of the herbivores. The numbers of eggs of *B. tabaci* on the third leaf from the bottom of the tomato plants was counted as an oviposition preference of *B. tabaci*. Tomato leaves selected by *F. occidentalis* were placed into the leaf cages as described above in survival rate section and the F1 nymph numbers of *F. occidentalis* in each cage was recorded every day until there were no new hatched nymphs, as an oviposition preference of *F. occidentalis*. There were ten replicates per choice combination in this experiment.

2.5 Statistical analysis

All data were checked for normality (Shapiro-Wilk test, $P < 0.05$) and homogeneity (Levene's test, $P < 0.05$) before statistical analysis. Data on the survival rate of herbivores were transformed to arcsine square root prior to statistical analysis. In addition, datasets that did not fit assumptions were arcsine square root transformed to meet the requirements of normality and equality of variances. The numbers of eggs of *B. tabaci* and the F1 nymph numbers of *F. occidentalis* were analyzed using generalized liner model (GLM), and means were compared using Fisher's least significant difference (LSD) test at $P < 0.05$ level. Paired samples (the feeding and oviposition preferences of herbivores, W vs R, W vs B or W vs RB choice groups) were tested using two-sided likelihood ratio test of GLM (Poisson distribution error with log link function) at $P < 0.05$ level. All other data were analyzed by one-way ANOVA ($P < 0.05$), and means were compared using Tukey's honest significant difference (HSD) test. All statistical analyses were performed using SPSS 25.0 (IBM, NY, USA) and graph plotting performed with GraphPad Prism 8.0 software (GraphPad Software, CA, USA).

3 Results

3.1 Effects of different light qualities on growth of tomato plant

Light quality significantly affected the growth (plant height, stem diameter and plant DW) of tomato plants. Compared with white light, red light significantly increased height of tomato plants, but blue and red-blue decreased it ($F = 1135.547$, $df = 3,23$, $P < 0.001$) (Fig. 1A). Blue light significantly inhibited the increase of stem diameter ($F = 14.314$, $df = 3,23$, $P < 0.001$), shoot ($F = 12.475$, $df = 3,23$, $P < 0.001$) and whole plant DW ($F = 12.149$, $df = 3,23$, $P < 0.001$) of tomato plant compared with white light (Fig. 1B, C).

3.2 Effects of different light qualities on leaf anatomy structure of tomato plants

Light quality significantly changed leaf thickness but had no effect on the main vein thickness of tomato leaves. Compared to the control, red light significantly reduced the thickness of tomato leaves but blue and red-blue light significantly increased leaf thickness ($F = 57.702$, $df = 3,23$, $P < 0.001$), which affected the leaf anatomy structure of tomato plants. Compared with white light, blue and red-blue light increased the thickness of the upper ($F = 13.846$, $df = 3,23$, $P < 0.001$) and lower epidermis ($F = 6.779$, $df = 3,23$, $P = 0.002$). The thickness of palisade tissue ($F = 47.827$, $df = 3,23$, $P < 0.001$) and spongy tissue ($F = 29.438$, $df = 3,23$, $P < 0.001$) increased significantly in the blue light treatments (Fig. 1D).

3.3 Effects of different light qualities on gas exchange traits and photosynthetic pigments of tomato plants

Light quality significantly altered the photosynthetic traits of tomato plants. Compared to white light, blue light significantly increased P_n of tomato leaves, while red light significantly decreased P_n ($F = 35.833$, $df = 3,23$, $P < 0.001$) (Supplementary Fig. S1A). Red light significantly decreased G_s ($F = 40.504$, $df = 3,23$, $P < 0.001$), C_i ($F = 10.870$, $df = 3,23$, $P < 0.001$), and T_r ($F = 24.982$, $df = 3,23$, $P < 0.001$) of tomato leaves. However, blue light significantly increased the G_s, and red-blue light significantly decreased *Ci* and T_r (Supplementary Fig. S1B, C, D). Furthermore, red-blue light significantly enhanced the contents of Chl a ($F = 16.061$, $df = 3,23$, $P < 0.001$), Chl b $F = 11.432$, $df = 3,23$, $P < 0.001$), and Chl a + b ($F = 14.627$, $df = 3,23$, $P < 0.001$) in tomato leaves. The Car content of tomato leaves increased significantly under blue and red-blue light, but significantly decreased under red light ($F = 18.999$, $df = 3,23$, $P < 0.001$) (Supplementary Fig. S1E).

3.4 Effects of different light qualities on photosynthetic products of tomato plants

The accumulations of photosynthetic products in tomato plants were significantly affected by light quality (Supplementary

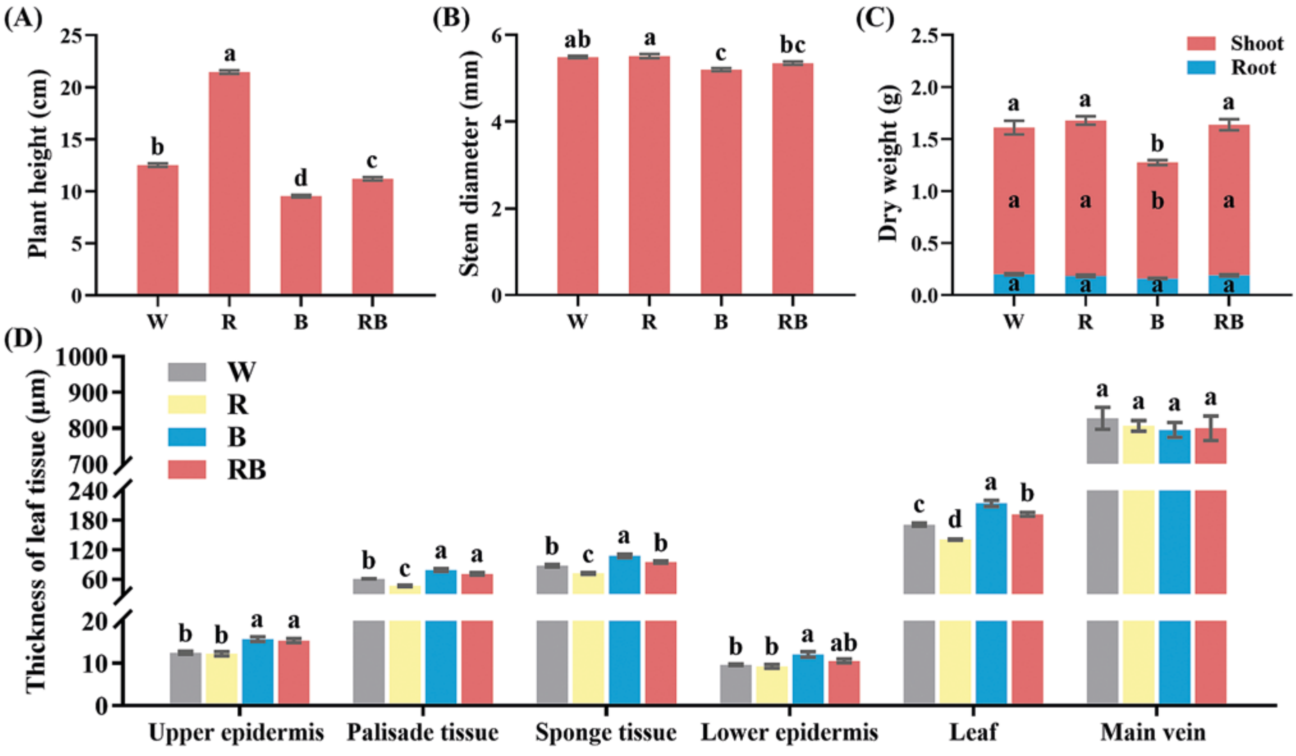

Fig. 1. Effects of different light qualities on growth and leaf anatomy structure of tomato plants. The plant height (A), stem diameter (B), dry weight (C), and leaf anatomy structure (D) of tomato plants under different light qualities for 15 days. Data in the figure are shown as means ± SE. Different small letters indicate that significant differences between different light quality treatments using one-way ANOVA followed by Tukey's HSD test ($P < 0.05$).

Fig. S1F, G, H). Compared to white light, blue light significantly reduced the accumulation of soluble sugar ($F = 8.787$, $df = 3,23$, $P = 0.001$) and starch ($F = 1418.439$, $df = 3,23$, $P < 0.001$) in tomato leaves but red and red-blue light did not significantly affect these parameters.

3.5 Performance of *Bemisia tabaci* on tomato plants treated with light qualities

There was no significant difference in the survival rate of *B. tabaci* after feeding on tomato plants treated with different light qualities, but it significantly affected the fecundity of *B. tabaci* (Fig. 2A, E). Compared with white light, the number of eggs of *B. tabaci* on tomato plants treated with red and blue light were significantly reduced ($\chi^2 = 42.938$, $df = 3$, $P < 0.001$). *Bemisia tabaci* showed a significant feeding ($\chi^2 = 11.174$, $df = 1$, $P = 0.001$) and oviposition ($\chi^2 = 18.524$, $df = 1$, $P < 0.001$) preference for tomato plants treated with white light rather than those treated by red light (Fig. 2B, F), and there was no feeding or oviposition preference for the test groups of W vs B and W vs RB (Fig. 2C, D, G, H).

3.6 Performance of *Frankliniella occidentalis* on tomato plants treated with light qualities

The survival rate of *F. occidentalis* feeding on tomato plants treated with different light qualities was not significantly affected, but their fecundity was significantly affected (Fig. 3A, E). Compared with white light, the F1 nymph numbers of *F. occidentalis* on tomato plants treated with red light reduced significantly ($\chi^2 = 40.968$, $df = 3$, $P < 0.001$). *Frankliniella occidentalis* showed a significant feeding ($\chi^2 = 14.212$, $df = 1$, $P < 0.001$) and oviposition ($\chi^2 = 10.962$, $df = 1$, $P = 0.001$) preference for tomato plants treated with white light over red-blue light (Fig. 3D, H). *Frankliniella occidentalis* had no feeding preference or oviposition preference for tomato choice combinations of W vs R and W vs B (Fig. 3B, C, F, G).

4 Discussion

The use of supplemental lighting technology for plants has been increasingly adopted to exploit and improve crop yield and quality in greenhouses. However, there have been few reports on its effects on plant suitability to insects (Kusuma et al. 2020; Lazzarin et al. 2021). In this study, we aimed to explore the effects of different light quality treatments on tomato plant growth and their defensive abilities against herbivores. We found that red, blue and red-blue light significantly affected the growth of tomato plants but had variable consequences on the performance of *B. tabaci* and *F. occi-*

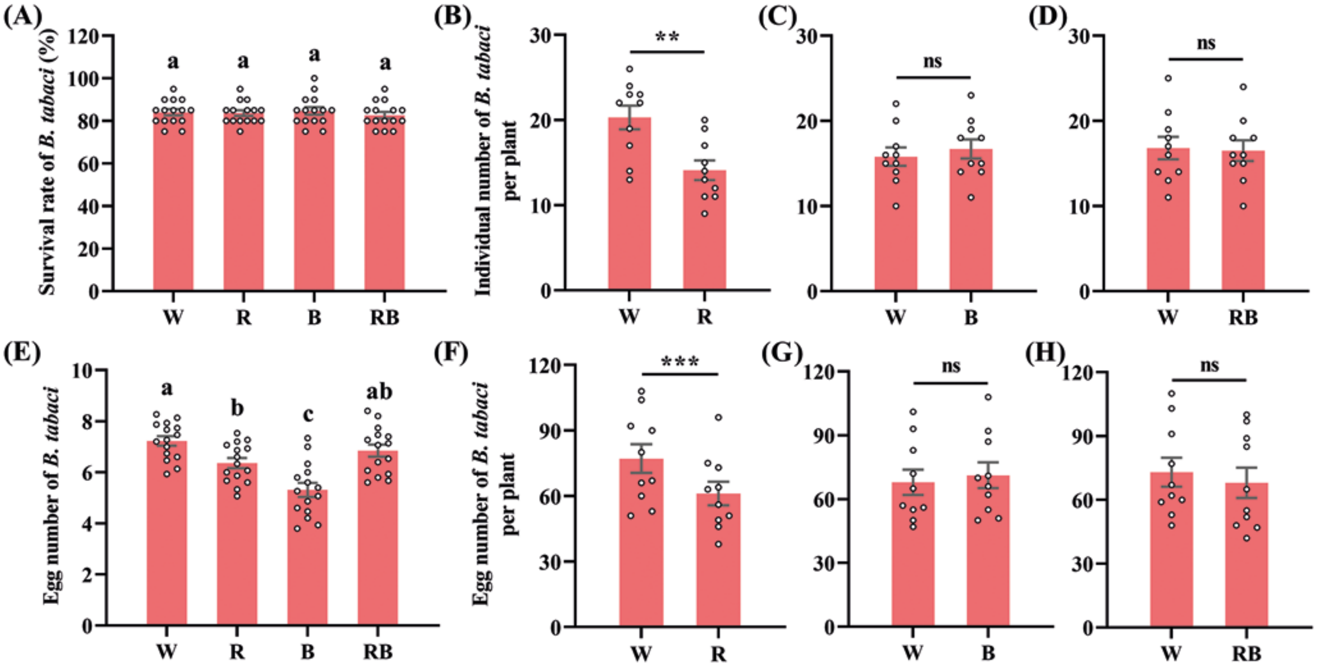

Fig. 2. Performance of *Bemisia tabaci* on tomato plants treated with different light qualities. Survival rate (A), feeding preference (B, W vs R; C, W vs B; D, W vs RB), fecundity (E), and oviposition preference (F, W vs R; G, W vs B; H, W vs RB) of *Bemisia tabaci* on tomato plants treated with different light qualities. Data in the figure are presented as means ± SE. For A and E, different small letters indicate that significant differences between different light quality treatments using one-way ANOVA followed by Tukey's HSD test, and GLM followed by Fisher's LSD test, respectively ($P < 0.05$). For B–D and F–H, the asterisk indicates that significant differences between different light quality treatments using two-sided likelihood ratio test with GLM (Poisson distribution error) at $P < 0.05$ level (**, $P < 0.01$; ***, $P < 0.001$; ns, not significant).

dentalis through the bottom-up effects of tomato plants (Han et al. 2015, 2022; Yang et al. 2024).

Our results show that different light qualities affect the growth of tomato plants. Compared with white light, red light promoted tomato plant height elongation, but blue and red-blue light inhibited plant growth but increased stem diameter. Similar results were observed in previous studies (Izzo et al. 2020; Kong et al. 2021; Yousef et al. 2021), indicating that different light qualities alter growth of tomato plants. In addition, light quality altered the dry matter accumulation of tomato plants. Blue light suppressed the shoot, root and whole plant dry weight compared to white light. This is consistent with the results of Izzo et al. (2020). The slight difference of red-blue light in previous studies may be due to the different PPFD ratio of red to blue (Izzo et al. 2020; Yousef et al. 2021). Taken together, this study showed that monochromatic light has the most obvious effect on plant morphological growth and biomass accumulation; red light can promote growth but blue light suppresses it and red-blue light has the least effect on plant growth.

Light quality could change the physical traits and anatomy structure of tomato leaves. Blue and red-blue light promoted the thickness of epidermis and palisade tissue, while red light inhibited it compared with white light. Similar results have been observed in previous studies (Li et al. 2021). The palisade and sponge tissue play important role in enhancing light penetration to the chloroplasts and improving light capture, respectively, thereby enhancing the photosynthetic traits of plants (Li et al. 2021). Compared with white light, red light decreased the P_n of tomato plants, blue light increased it, which is consistent with previous study (Kong et al. 2021). Photosynthetic pigment is indispensable for plants to absorb, transfer and convert light energy to bioenergy and plays a crucial role in the photosynthesis process (Blankenship 2010; Liu et al. 2021). The increase of chlorophyll and carotenoids were an important reason for increases in photosynthesis, especially in blue light (Croft et al. 2017). This increase in photosynthesis and related parameters, which did not increase tomato plant growth and biomass under blue light, may be caused by the loss of leaf area, photodamage, photoinhibition and rubisco enzyme activity (Blankenship 2010), which should be verified in future experiments.

The growth and biomass of tomato plants under blue light were significantly inhibited and this could be due to differences in the accumulation of photosynthetic products. Blue light significantly reduced the accumulation of soluble sugars and starches. Soluble sugars and starches are the primary energy substance and signaling molecules of many plants

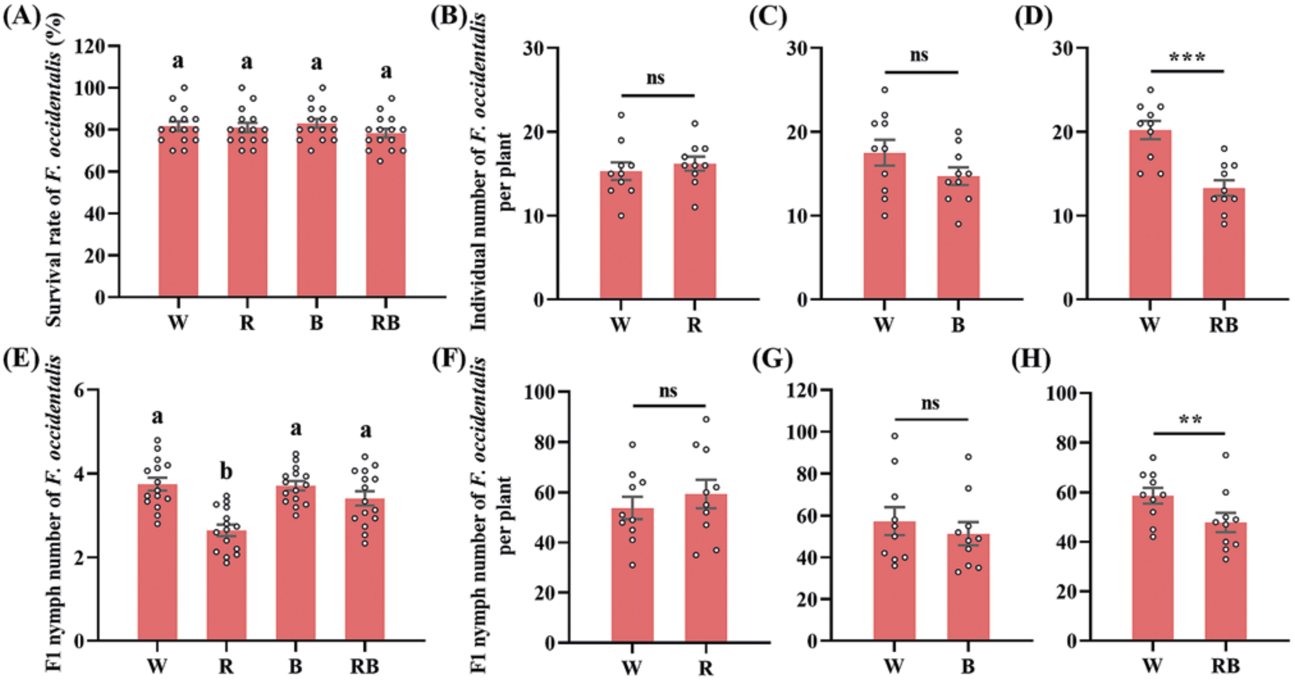

Fig. 3. Performance of *Frankliniella occidentalis* on tomato plants treated with different light qualities. Survival rate (A), feeding preference (B, W vs R; C, W vs B; D, W vs RB), fecundity (E), and oviposition preference (F, W vs R; G, W vs B; H, W vs RB) of *Frankliniella occidentalis* on tomato plants treated with different light qualities. Data in the figure are presented as means ± SE. For A and E, different small letters indicate that significant differences between different light quality treatments using one-way ANOVA followed by Tukey's HSD test, and GLM followed by Fisher's LSD test, respectively ($P < 0.05$). For B–D and F–H, the asterisk indicates that significant differences between different light quality treatments using two-sided likelihood ratio test with GLM (Poisson distribution error) at $P < 0.05$ level (**, $P < 0.01$; ***, $P < 0.001$; ns, not significant).

and plays an important role in plant growth, development and biomass composition (Li & Sheen 2016; Mishra et al. 2022), which led to the suppression of growth and biomass accumulation of tomato plants under blue light. Light quality therefore altered the growth of tomato plants, particularly the physical traits of leaves, which would also affect the defensive ability of tomato plants and have an impact on the performance of herbivores (Fernandez-Milmanda et al. 2020; Lazzarin et al. 2021).

Light quality improved the defensive ability of tomato plants and had a negative effect on the performance of herbivores through the bottom-up effects. The fecundity and feeding and oviposition preference of *B. tabaci* and *F. occidentalis* on tomato plants treated with different light qualities were altered. The fecundity of *B. tabaci* and *F. occidentalis* on host plants depends on the nutritional quality, defensive chemicals/metabolites composition and content of host plants (Konan et al. 2024; Kumaraswamy et al. 2024; Zhu et al. 2024). For example, flavonoids, an important defensive compound, protect plants against herbivores by affecting the growth, development and behavior of insects (Zhang et al. 2020; Xia et al. 2021). The biosynthesis of flavonoids can be enhanced through the addition of red and blue light but reduced by far-red light (Lazzarin et al. 2021).

Plant defense mechanisms are generally regulated by endogenous phytohormonal signal-transduction pathways, including SA and jasmonic acid (JA) signaling pathways (Wu & Baldwin 2010; Ye et al. 2021). An increasing number of studies have shown that the basic SA level increased by red and blue light that enhance defensive intensity, subsequently improving plant resistance to *B. tabaci* (Wang et al. 2023; Yang et al. 2023). Low R: FR ratio light can induce the formation of inactive HSO_4-JA by catalyzing the activity of sulfotransferase, and reduce the level of active JA, thus reducing the intensity of plant defense responses against *S. littoralis* (Fernández-Milmanda et al. 2020). It can therefore be speculated that red light induces the increase of JA and SA levels, antioxidant enzymes and other defense chemicals in tomato, increasing resistance to *F. occidentalis* (Courbier et al. 2020). Additionally, red (but not white) light induced-tomato plants significantly repelled feeding and oviposition of *B. tabaci* while red-blue (but not white) light induced-tomato plants significantly repelled feeding and oviposition of *F. occidentalis* females. This may be due to high JA levels in both red and red-blue light induced-tomato plants, which can activate defense-related terpenoids and green leaf volatiles (Mirzahosseini et al. 2020). However, the reasons for the effects of red, blue and red-blue light induced-tomato plants on the fecundity and choice preference of *B. tabaci* and *F. occidentalis* need further investigation.

In this study, we found that different light qualities significantly altered the growth and defensive ability of tomato plants to differing degrees. Since tomato plants treated with red and red-blue light showed inhibitory effects on the performance of *B. tabaci* and *F. occidentalis*, these two lights could be used as supplementary lighting in facilities to reduce the performance of herbivores on tomato plants, improving the yield and quality of tomato plants. Our findings allow supplementary lighting in facility agriculture to combine both growth and defense of crops, and provide a better application and theoretical basis of artificial supplementary light in the production of facility agriculture.

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Figure S1